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Reshaping our understanding of species' roles in landscape-scale networks

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Abstract

In network ecology, landscape-scale processes are often overlooked, yet there is increasing evidence that species and interactions spill over between habitats, calling for further study of inter-habitat dependencies. Here we investigate how species connect a mosaic of habitats based on the spatial variation of their mutualistic and antagonistic interactions using two multilayer networks, combining pollination, herbivory and parasitism in the UK and New Zealand. Developing novel methods of network analysis for landscape-scale ecological networks, we discovered that few plant and pollinator species acted as connectors or hubs, both within and among habitats, whereas herbivores and parasitoids typically have more peripheral network roles. Insect species' roles depend on factors other than just the abundance of taxa in the lower trophic level, exemplified by larger Hymenoptera connecting networks of different habitats and insects relying on different resources across different habitats. Our findings provide a broader perspective for landscape-scale management and ecological community conservation.

Introduction

Ecological networks provide a framework to describe species' roles within ecological communities by compiling the biotic environments of co-occurring species (Cirtwill *et al.*, 2018). In particular, meso-scale network analyses of species' interactions highlight two functionally important species types: “hubs”, highly generalist species forming the core of ecological networks and consistently interacting with multiple species over space and time (Olesen *et al.*, 2007), and “connectors”, ensuring cohesion by linking species groups together (González *et al.*, 2010). Hence, as not all species contribute equally to ecosystem function and stability, some could be targeted for ecological management purposes based on their critical role in a community (Montoya *et al.*, 2012; Cirtwill *et al.*, 2018).

Fuelled by widespread habitat changes, ecological research and management is often scaled up to a landscape level, allowing a wider understanding of effects on landscape-scale biodiversity and ecosystem functioning (Haddad *et al.*, 2015). Ecological networks provide a means of understanding how management practices or perturbations can percolate through ecological communities (Harvey *et al.*, 2017) by outlining the characteristics of key species necessary for community functioning in, for example, fragmented landscapes (Hagen *et al.*, 2012; Grass *et al.*, 2018; Emer *et al.*, 2018). Broadening the approach to other multi-habitat landscapes and increasing the spatial scale of network studies captures more species and interactions (Galiana *et al.*, 2018), with habitat diversity generating novel architectures (Pillai *et al.*, 2011; Peralta *et al.*, 2017). Species dynamically link networks in different adjacent habitats (McCann *et al.*, 2005; Frost *et al.*, 2016), and identifying key species could illuminate how ecological communities might respond to alterations in landscape structure and habitat diversity (Montoya *et al.*, 2012; Evans *et al.*, 2013). Currently though, we lack general rules for identifying species that drive cross-habitat linkages which take into account both species' trophic and habitat generalisation.

Achieving this understanding for communities that combine different interaction types poses some difficulties. Some species could have consistent roles across interaction types: plants pollinated by many insect species may also be consumed by many herbivore species thus they may be a generalist for both interaction types (Sauve *et al.*, 2016). In such cases, their extinctions could affect both networks similarly (Pocock *et al.*, 2012). However, species involved in different interaction types can also respond differently to environmental gradients. Consequently, mutualist and antagonist insects could occupy different network roles within and across habitats (Tylianakis

& Morris, 2017). Distinguishing between these hypotheses has been difficult, because empirical datasets combining multiple interaction types across different habitats are virtually non-existent (but see Pocock *et al.*, 2012). It is unclear how well species roles can be generalised across interaction types and multiple habitats, and what mechanisms are driving the spatial architecture of ecological networks.

Despite this, we can make general predictions about species' positions in ecological networks and the mechanisms driving their roles. First, plant species composition influences species diversity and abundance in higher trophic levels (Scherber *et al.*, 2010). Abundant species tend to interact as generalists because they are more likely to encounter interaction partners (Fort *et al.*, 2016). Therefore, abundant plant species are more likely to be hubs. Second, we expect insect species are able to link habitats through their movement (Macfadyen & Muller, 2013; Devoto *et al.*, 2014). Typically, larger pollinators have higher mobility and a more generalist diet (Greenleaf *et al.*, 2007; Fontaine *et al.*, 2009), implying the ability to connect ecological communities or habitats. Mobile insects might link habitats by exploiting different resources in different habitats, while the effect of diet could propagate to higher trophic levels, such that herbivore roles could predict their parasitoids' role.

Our aim here is to understand how species connect a mosaic of habitats based on the spatial variation of their interactions. We sampled in two multi-habitat landscapes, combining multiple interaction types (mutualistic and antagonistic) between plants and insects with two objectives: 1) We present a new method to determine plant, pollinator, herbivore and parasitoid species' roles in landscape-scale networks containing multiple interaction types. 2) We examine the contribution of different potential drivers (plant species abundance, insect species mobility and varied diet) to species' identified roles. An assumption behind our objectives is that plant assemblages drive insect species' foraging behaviour and therefore their roles. Thus, we further this second objective with a null model approach to test the degree to which species roles are determined solely by their resources' distribution across the landscape.

Material and methods

Field sites

Fieldwork was conducted in two countries and both sites were ocean-adjacent peninsulas consisting of a mosaic of habitats:

1) Hengistbury Head in the United Kingdom ($50^{\circ}4'59.67''\text{N}$ $1^{\circ}45'22.74''\text{W}$, 162 ha in size), contains seven habitats: grassland, heathland, woodland, salt marsh, scrub, reed bed and sand dune (Fig. 1), and was sampled twice a month from June to September, 2013.

2) Tautuku Peninsula in New Zealand ($46^{\circ}35'30.68''\text{S}$ $169^{\circ}25'39.46''\text{E}$, 225 ha in size) consists of five habitats: Coprosma scrub, Mānuka scrub, salt marsh, woodland and sand dune (Fig. 2). This site was sampled twice a month from November 2014 to February 2015.

At both sites, we selected two plots in each of their constituent habitats, each plot delimiting an area equivalent to 5% of each habitat's area, so that a total of 10% of each habitat is sampled. We pooled the data to create ecological networks at a larger spatial scale (as in Macfadyen *et al.*, 2009).

Data collection

We sampled each plot monthly for interactions involving plants, flower visitors, leaf-miners, seed-feeding insects and parasitoids, randomly choosing one of the two plots in each habitat to sample first. While an insect visiting a flower does not necessarily equate to a pollination event, here we assume it is an appropriate proxy for pollination (Vázquez *et al.*, 2005).

Plant data. We placed a 50 m transect line at a randomly selected start point and direction in each plot on each visit. To estimate the floral resources, we placed a 0.5 m² gridded quadrat every 10 m on alternating sides of the transect and within this we identified all flowering herbaceous plants to species and counted the number of open floral units. We quantified vegetation cover by calculating a percentage cover of each plant species observed in the quadrat from two measures on plant abundance: the number of times a plant species touched the 36 cross-points of the gridded quadrat, as well as a categorical vegetative cover measurement (see Appendix S1).

Herbivore and parasitoid data. We sampled two guilds of herbivores, leaf miners and seed feeders, along with the plants they fed on and the parasitoids that attacked them. Leaf miners were sampled

from a 1 m² quadrat placed every 10 m on alternating sides along the transect line in each plot, searching up to 2 m high in vegetation. We collected all leaves with leaf miner larvae and identified leaf miners from the leaf mine pattern. Miners were reared individually until emergence of either leaf miner adults or parasitoids (Pocock *et al.*, 2012, Appendix S1). We focused our sampling of seed-feeding insects on those feeding on 9 species of plant on Hengistbury Head and 10 on Tautuku Peninsula collecting up to 50 seeds per species per transect. These plants were identified as the species most likely to host seed feeders from previous studies in the UK and those with similar seed heads in NZ (Pocock *et al.*, 2012, Appendix S1). Seeds were collected from within 10 m of the transect line and were collected from multiple plants and locations along the transect line, where possible. Seed herbivores were reared collectively until adult herbivores or parasitoids emerged. All reared insects were identified to species by taxonomists (see acknowledgements, Appendix S1). Parasitised seed-feeding insects were destroyed before emergence so linking parasitoids to specific seed feeders was impossible. Thus seed-feeding herbivores and their parasitoids both link directly to plant species in our networks.

Pollinator data. Interactions between flower visitors and plants were sampled by haphazardly walking for 30 minutes in each plot between 9:00 and 17:30 during dry, warm conditions (at least 15°C), and low wind conditions. All insects seen on flowers were collected, the interaction recorded and the insect identified to species by taxonomists (see acknowledgements).

Construction of the multilayer networks

For each site, we compiled data on species interactions into a set of networks, each describing within-habitat interactions quantified with interaction frequencies. Together, they describe a multilayer landscape network of habitat-scale networks with each layer representing a habitat (Pilosof *et al.*, 2017, see Appendix S2). Multiple interaction types were normalised by scaling all interaction frequencies so that each interaction type had the same range of interaction weights (as in Sauve *et al.*, 2016). Without such scaling, highly frequent floral-visitation events would outweigh other types of interactions (Fontaine *et al.*, 2011), obscuring the identification of important species.

For each of our multilayer networks, a three-dimensional array $B = (B_{ijh})_{i \in [1, S], j \in [1, S], h \in [1, N]}$ describes interactions among the S species within each of the N habitats, with non-zero elements depicting observed interactions. We define the quantification function q so that $q(B_{ijh})$ is the weight

of the interaction between species i and j in habitat h .

Defining species' roles in landscape-scale networks

To separate species according to their role in the landscape, we characterised their relative importance within habitats with respect to their habitat generalism. Two metrics capture these features for each species i : within-habitat weight z_i , and among-habitat connectivity c_i . Both account for species' observations in multiple habitats, dividing the community into subsets sharing species. This approach draws on Guimera and Amaral's (2005) framework, but includes fuzzy partitioning of species across habitats while taking into account the interaction weights in each habitat as follows:

1) The within-habitat weight z_i of species i measures how important each species is in the landscape, due to strong and/or multiple interactions. Species' weights are aggregated in each habitat. Thus, it is the weighted-arithmetic mean of the local within-habitat weights z_{ih} , and is written $z_i = \sum_h \beta_{ih} z_{ih}$ with z_{ih} calculated as the z-score of the weight of species i in habitat h . The belonging coefficient β_{ih} of species i to habitat h is the ratio of its interaction weight $\sum_j q(B_{ijh})$ in habitat h over its total weight in the landscape.

2) The among-habitat connectivity c_i measures how evenly distributed the interactions of species i are in the landscape, and is calculated as $c_i = 1 - \sum_h \beta_{ih}^2$. c_i tends towards 1 if interactions are distributed evenly among the habitats and towards 0 if interactions occur in a single habitat.

These two metrics define a plane in which we identify four groups of species corresponding to landscape-scale network roles according to their relative $\{z_i, c_i\}$ -values (Fig. 3A). First, we define hubs as the most generalist species, having a high z_i . As z_i are based on z-scores, we set a discriminative threshold at $z_i = 2.576$, the critical value for a significance level $\alpha = 0.005$, hence fixing the chance of type I error. Second, we identify species with high connectivity if their belonging coefficients to various habitats are all lower than 60%. Thus, the upper among-habitat connectivity boundary is the value required for the 40% of interactions remaining to be equally assigned to the $N - 1$ other habitats. This threshold depends on the number of habitats forming the landscape and is $c_i = 0.6133$ for Hengistbury head, and $c_i = 0.6$ for Tautuku Peninsula (see Appendix S2).

With these two thresholds, four species roles emerge in the $\{z_i, c_i\}$ -space (c.f. Fig. 3B-C). Among hubs ($z_i \geq 2.576$), we distinguish habitat hubs which are locally important species ($c_i \leq$

$\{0.6133, 0.6\}$ and $z_i \geq 2.576$), and landscape hubs which are highly connected species in multiple habitats ($c_i > \{0.6133, 0.6\}$ and $z_i \geq 2.576$). Among non-hubs ($z_i < 2.576$), we discriminate peripheral species which have most of their interactions in a given habitat ($c_i \leq \{0.6133, 0.6\}$ and $z_i < 2.576$), from habitat connectors, interacting more equally across multiple habitats ($c_i > \{0.6133, 0.6\}$ and $z_i < 2.576$).

Nonetheless, because we heuristically defined them, these thresholds are indicators of species' ability to connect habitats or support multiple interactions within one or multiple habitats, rather than strict boundaries between species roles.

Investigating drivers of species' roles

To test whether abundant plants tend to be classified as hubs, we used a Spearman rank test for a correlation between estimates of plant species abundance, X_i , and their intra-habitat weights z_i . To assess the distribution of plant species i in the landscape, we calculated a weighted-arithmetic mean of its z-scored abundance X_i . Plant abundance was calculated as the quantity of resources they provide for flower-visiting, leaf-mining and seed-feeding insects. We used the number of floral units as an approximate measure of the floral resources available to flower-visitors and seeds to seed-feeders, and the percentage of vegetative cover as an approximation of the vegetative resources available for leaf-miners (see Appendix S1).

Body size correlates with the foraging range of flower-visiting Hymenoptera (Greenleaf *et al.*, 2007); this finding was extended to flower-visiting Diptera, Lepidoptera and Coleoptera to estimate insects' mobility (Baldock *et al.*, 2019). Using the same approach, we measured the intertegular distance for Hymenoptera, Diptera and Lepidoptera; for Coleoptera, we measured the length of the elytra and width at the widest point. Where possible, 10 individuals were measured and a mean value used. Fifty four percent of flower visiting species had been already measured by Baldock *et al.* (2019) thus we just measured the remaining species. We only considered flower visitors for body size analysis, in order to avoid complications due to herbivore hosts being destroyed by their parasitoids and size variation within parasitoid species being due to variation in host size. For each pollinator order, we tested for a correlation between species' inter-habitat connectivity, c_i , and its average mobility estimate using a Spearman rank correlation.

Additionally, we explored whether a species' use of a different set of resources/hosts in each

habitat (i.e. diet generalism) affects its network role. We tested for a correlation between the mean dissimilarity of diets across habitats and the Shannon diversity of resources/hosts for each insect species foraging at the landscape scale (Blüthgen *et al.*, 2008). To calculate the mean dissimilarity of diets across habitats, we compare local diets using Bray-Curtis’s dissimilarity metric, comparing the diet of the focal species within each habitat with its diet aggregated at the landscape scale (see Appendix S3). Lower values correspond to diets with overlapping resources across habitats, while higher values reflect diets comprised of different resources in each habitat. We performed a Wilcoxon rank-sum test comparing dietary dissimilarity across habitats between species with high among-habitat connectivity and those with low connectivity.

Finally, we tested whether the role of parasitoid species can be predicted by their hosts. We used linear models to evaluate how within-habitat weight of hosts and among-habitat connectivity explains the values of their parasitoids.

The null model

We tested whether species positions in the $\{z_i, c_i\}$ -plane are significantly different from insects randomly foraging in the landscape using a null model assuming a bottom-up assemblage driven by plant abundance and distribution. The resulting landscape-scale ecological networks preserve the plant composition in habitats, and avoid the creation of forbidden links between species (Vázquez *et al.*, 2009) while maintaining the total number of interaction events observed in the landscape. Therefore, the probability of an interaction event depends on the identity of the interaction and the local abundances of the resource species. While the topology of the aggregated network is maintained, the local networks may differ between the observed and the expected. Differences highlight non-random structuring processes (e.g. habitat or resource preferences) and interactive effects (e.g. exploitative competition) (see Appendix S4). To avoid biases related to multiple testing, we calculated the probability of observing the exact number of significant tests (i.e. a species has a position in the $\{z_i, c_i\}$ -plane that is different than expected with the null model), using the probability mass function of the binomial distribution (Moran, 2003).

All analyses were performed, and figures created, using R (R Core Team, 2018). The code for building landscape-scale networks, calculating $\{z_i, c_i\}$ -values, and generating networks following null models are available at <https://github.com/alixsauve/Landscape-species-roles>.

Results

Overview of networks and species roles

We sampled 56 species of plant and 314 species of insect from Hengistbury Head, with 2,236 insects collected. These comprised: 217 flower-visiting species, 55 herbivore species and 39 parasitoid species; three insect species were observed in more than one interaction type. Tautuku Peninsula was more sparsely populated with 37 species of plant and 96 species of insect with 575 individuals caught and 53, 25, and 18 species of flower visitors, herbivores and parasitoids, respectively. Seven species were found in both the British and New Zealand webs, these being introduced alien species from the UK to New Zealand. For each site, a map and its constituent habitat networks is shown in Fig. 1 and 2, and network descriptors are presented in Appendix S5.

Combining the within-habitat weight and the among-habitat connectivity, species are classified as follows (Fig. 3B-C): Peripheral species represent a large proportion of species (86.2% for Hengistbury Head, and 96.2% for Tautuku Peninsula). In particular, most leaf-mining and seed-feeding insect species are classified as such (94.5% and 96% for Hengistbury Head and Tautuku Peninsula respectively, see Appendix S6). Habitat connectors represent a small proportion of species in Hengistbury Head (10.5%) and are predominantly flower visitors (84.6%). In contrast, no strong habitat connectors are reported for Tautuku Peninsula. Habitat hubs are rare (3% and 3.7% of species in Hengistbury Head and Tautuku Peninsula, respectively; Appendix S6), and insects identified as such are few (6 and 2 species in Hengistbury Head and Tautuku Peninsula, respectively). Only one landscape hub is highlighted for Hengistbury Head, the plant *Hypochaeris radicata*, while none are found at Tautuku Peninsula (Appendix S6).

Drivers of species' roles

The within-habitat weight of plants is not correlated with their abundance at Hengistbury Head (Fig. 4A). Neither the number of floral units ($\rho_{52} = 0.16$, $p > 0.05$), nor the percentage cover ($\rho_{52} = 0.19$, $p > 0.05$) correlates with the within-habitat weight of plant species there (Fig. 4A). Tautuku Peninsula's data suggest a different trend: while the number of floral units does not correlate with the within-habitat weight of plants ($\rho_{35} = 0.01$, $p > 0.05$), the percentage cover is positively correlated with it ($\rho_{35} = 0.45$, $p = 0.005$, Fig. 4B). When looking at the within-

habitat weight for each habitat separately, these results change with the habitat (see Appendix S7), suggesting that the effect of plant abundance is context-dependent.

Our null model does not explain a large proportion of the plant species positions in the $\{z_i, c_i\}$ -plane, in either Hengistbury Head or Tautuku Peninsula (66% of plant species; $p < 0.001$ for Hengistbury Head, and 40.5%; $p < 0.001$ for Tautuku Peninsula, Fig. 3B-C) meaning that plant abundance and distribution, combined with plants' ability to attract insect species are insufficient to predict plants species' role in the landscape. However, some plant species stand out as peripheral species strongly linked to a specific habitat (Fig. 3C), or as habitat hubs which are locally preferred by insect species (Fig. 3B, Appendix S6).

For Hymenoptera, there is a positive correlation between the among-habitat network connectivity and their intertegular span (Fig. 5C, $\rho_{53} = 0.56$, $p < 0.001$), but not for Coleoptera, Diptera, and Lepidoptera (elytra length: $\rho_{19} = -0.12$, $p = 0.60$; elytra width: $\rho_{19} = 0.12$, $p = 0.61$; $\rho_{167} = -0.03$, $p = 0.72$; $\rho_{13} = -0.03$, $p = 0.91$, Fig. 5A-B-D).

The dissimilarity of diet for insect species in each habitat versus at the landscape-scale is positively correlated with their diet breadth both in Hengistbury Head and Tautuku Peninsula (Fig. 6A; $\rho_{306} = 0.79$, $p < 0.001$ for Hengistbury Head, Fig. 6B; $\rho_{94} = 0.68$, $p < 0.001$ for Tautuku Peninsula). Thus, insect generalism at both locations is a consequence of dissimilar diets combined from multiple habitats. Species with high connectivity had significantly more dissimilar diets across habitats than those with low connectivity ($U_{35,279} = 9343$, $p < 0.001$ in Hengistbury Head).

The within-habitat weights of hosts predict their parasitoids' within-habitat weight ($t_{55} = 5,278$; $p < 0.001$; $slope = 0.53$; $R_{55}^2 = 0.33$; see Appendix S8), but this was not the case for the among-habitat connectivity ($t_{55} = 1.289$; $p = 0.20$; $slope = 0.2$; $R_{55}^2 = 0.029$; see Appendix S8).

A sizeable proportion (51.6%; $p < 0.001$ for Hengistbury Head and 27%; $p < 0.001$ for Tautuku Peninsula) of insect species' positions in the $\{z_i, c_i\}$ -plane was not explained by our null model, suggesting that the distribution of insect species and their interactions across the landscape cannot be predicted solely by plant distributions at both sites (Fig. 3B-C). At both sites, some insect species that are classified as peripheral or habitat hubs have $\{z_i, c_i\}$ -values differing from null expectations (see Appendices S4 and S6).

Discussion

Our analysis of landscape-scale ecological networks sheds light on species' roles in a mosaic of habitats. First, most hubs are plant species, but these roles were not always explained by their higher abundance in the landscape. Second, habitat connectors tend to be the most generalist insect species, feeding on a variety of resources across habitats. However, only in Hymenopteran pollinators does an insect's ability to fly long distance correlate with their ability to connect habitats. Third, insects do not necessarily forage where their resources and hosts are the most abundant, suggesting an influence of insects' habitat preference and possibly interactive or other unmeasured effects.

Hub species were rare at both sites and are a mix of plants and insects. Plants being habitat hubs could be the result of plant assemblages being a main criterion for distinguishing specific habitats (e.g. Joint Nature Conservation Committee Habitat Classifications, Phase 1 Habitat Classification, UK Biodiversity Action Plan, the Land Cover Database in NZ), and the bottom-up sampling of networks. Some plants that emerge as habitat hubs are biologically restricted to that habitat (e.g. *Aster tripolium* in Hengistbury Head salt marsh or *Pimelea lyallii* and *Samolus repens* on Tautuku Peninsula sand dune and salt marsh, respectively), or are a defining feature (e.g. *Calluna vulgaris* for heathland). The only landscape hub at Hengistbury head was *Hypochaeris radicata*, a member of Asteraceae, which was widespread at both study sites. This successful coloniser is common in Europe and considered invasive in Austral-Asia (Ortiz *et al.*, 2008).

The major role of plants in landscape-scale ecological networks can filter up to their interacting insects. Thus, at Hengistbury Head, some habitat hubs were highly specialised leaf miners, for example *Phytomyza ilicis*, *Bucculatrix maritima*, and *Emmetua marginea* feeding on *Ilex aquifolium*, *A. tripolium*, and *Rubus sp.*, respectively. In turn, their parasitoids (*Apanteles maritimus* and *Chrysochaeris gemma* for the latter two) stand out as significant natural enemies in these habitats. Hence, plants as habitat hubs can be the root of major trophic chains in the landscape. Insect hubs are detectable only when accounting for interaction weights though, being classified as peripheral in qualitative analysis of species' roles (see Appendix S9).

However, plant-based habitat distinctions may not equate to distinct animal communities (Timóteo *et al.*, 2018). Here, pollinators represent a large proportion of habitat connectors, meaning that these species forage in multiple habitats; this mobility could impact ecosystem stability

(Rooney *et al.*, 2006). Landscape management, particularly for pollinators, often focuses on preserving connectivity among patches of similar habitat type (e.g. Hanski & Ovaskainen, 2000; Grass *et al.*, 2018), but pollinators connecting various habitat types together indicate species' dependence on multiple habitats (e.g. Mandelik *et al.*, 2012). Avoiding discontinuity in resource provision is a major requirement for pollinator conservation and protection of related ecosystem services (Schellhorn *et al.*, 2015). Landscape-scale management of ecological networks thus provides a method of reaching this goal by identifying which key habitats pollinators need.

The vast majority of herbivores and parasitoids act as peripheral species at both sites. This result is most likely a consequence of herbivores' specialisation and/or dependence on a certain habitat. Herbivore specialisation, both on habitats and resources, drives specialisation of their parasitoids, resulting in them also being habitat-constrained and sensitive to landscape structure (Roland & Taylor, 1997). This result contrasts with the “cross-habitat spill-over hypothesis”, an expectation in biological pest control, whereby natural enemies, including parasitoid species, move between habitats (Tscharntke *et al.*, 2008, 2012) in response to changes in their hosts' abundance (Frost *et al.*, 2015), leading to cross-boundary pest-control (Frost *et al.*, 2016). In an agricultural context, while parasitoids of leaf miners physically move between habitats, they do not always interact with hosts in both adjacent habitats; rather they could use the adjacent habitat as a refuge or for floral resources (Macfadyen & Muller, 2013). This could explain the differences between our results and previous studies involving similar vegetation structure and high host overlap among habitats (Frost *et al.*, 2015, 2016). Most likely, parasitoid spill-over depends on the identity of neighbouring habitats (Inclán *et al.*, 2015) and their differences in primary production (Frost *et al.*, 2015).

At both sites, especially Tautuku Peninsula (NZ), we detected very few hubs and connectors with most species identified as peripherals. This distribution of species' roles questions whether the species most important to landscape-scale conservation efforts, hubs and connectors, are genuinely rare or whether we fail to effectively identify them. Hubs are detectable at lower sampling efforts yet increasing sampling effort might enhance detection slightly (see Appendix S10). Identifying connector species is more sensitive to sampling effort as this relies on detection of interactions in multiple habitats (see Appendix S10), thus increasing the required sampling time. This could stem from the patterns of resource availability over space and time. For species with multiple generations

per year or long life-spans, crossing habitats may be necessary to fulfil their foraging requirements (Mandelik *et al.*, 2012; Tschardtke *et al.*, 2012). However, evidence of cross-habitat spill-over does not necessarily imply landscape hubs and not all landscapes are equally conducive to cross-habitat foraging species (Inclán *et al.*, 2015; González *et al.*, 2016). Consequently, while potentially a good indication, our methods might not provide a complete identification of all hubs and connectors central to a management plan.

After identifying species' roles, we combined the use of a null model with species traits to explore how these roles arise. First, plant species' abundance alone was insufficient to explain their role or those at higher trophic levels, a result mirrored by the general lack of correlation between plant and floral abundance and the within-habitat weight. Landscape-scale management actions should therefore not focus only on most abundant taxa but also target key species identified by combining our null model with our method to identify species' roles (see Pocock *et al.*, 2012 for similar considerations using robustness analyses). Differences between observations and null expectations highlight the important role of additional factors such as insect mobility, and habitat and dietary preferences.

Second, because our null model did not account for insects' mobility, the deviation of observed results implies that mobility between habitats might vary between species. Among Hymenoptera, larger bees were more likely to have higher among-habitat connectivity, in line with Greenleaf *et al.* (2007). Many Hymenoptera, particularly bumblebees and honeybees, are central place foragers and must gather resources to bring back to the nest (Kacelnik *et al.*, 1986). Therefore, travelling farther to maximise nectar and pollen load would encourage more variable interactions in multiple habitats (Osborne *et al.*, 2008). Moreover, social bees are likely to be more active than species foraging solely for themselves; this could result in greater connectivity across the landscape. There was no link between body size and tendency to connect habitats in any other insect order. Nonetheless, we cannot exclude 'passive' spill-over as small insects may undergo wind-borne dispersal (Tschardtke *et al.*, 2005). Our results do not preclude that other unmeasured traits are important in determining the tendency to connect habitats (e.g. life span), or to specialise on one (e.g. breeding requirements, food plant, predator protection).

Third, there was a strong positive correlation between the ability of insect species to connect habitats and the variability of the diet of generalists across habitats. Pollinators, as well as herbi-

vores and parasitoids, may find different resources in different habitats. For pollinators this is most likely due to phenology, with species moving from one habitat to another as the availability of floral resources in each habitat changes. This could also be influenced by specific biological preferences as well as the suitability of some plants for certain life stages of the herbivores (Vaudo *et al.*, 2015). Using mean values for each species could miss details regarding the distribution of interactions over the landscape; however, complementary analysis using linear mixed models shows broadly similar trends (see Appendix S3). Insects are likely to have uneven preferences for resources/hosts (Staniczenko *et al.*, 2013), which may depend on the habitat where the interactions occur (Staniczenko *et al.*, 2017; see Appendices S4 and S7). For instance, parasitising behaviour translates into variable interaction frequencies depending on the habitat type (Staniczenko *et al.*, 2017). Similarly, other insect species may swap resources between habitats, because of changes in competitors rather than in interaction partners (Poisot *et al.*, 2012). Hence, interactive effects could also explain observed deviations from expected roles.

Conclusion

Species' roles are driven by a combination of factors including network properties (i.e. how well-linked a species is versus its tendency to connect different habitats) and specific lifestyle requirements constraining certain species to particular habitats. Thus network ecology could be a valuable tool in ecological management of heterogeneous mosaics of habitats. Our approach is applicable to multi-habitat landscapes and, more generally, the wider field of metaecology (Schiesari *et al.*, 2018). Whether focusing on increasingly fragmented or homogenised landscapes, elucidating species' roles complements a dynamic understanding of metacommunities – for instance, habitat connectors are most likely to contribute to stability (McCann *et al.*, 2005; Rooney *et al.*, 2006), and their roles may be partly explained by density-dependent processes (Hagen *et al.*, 2012). Understanding species' roles in landscape-scale networks improves our perception of species' importance and how best to support ecosystem services through diverse, connected habitats. A better comprehension of which landscape configurations benefit from the emergence of functionally important species could have far reaching effects in both conservation and restoration ecology.

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Statement of authorship

The study was conceived by JM and DM and designed with input from all authors. Fieldwork was carried out by TDH and ND; methods to identify species roles in the landscape were developed by AMCS, AMCS and TDH carried out the analyses. AMCS and TDH led the writing of the manuscript, all authors contributed to drafts of the manuscript and gave final approval for publication.

Data accessibility statement

Data supporting the results are publicly available on Figshare Repository:

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Figures

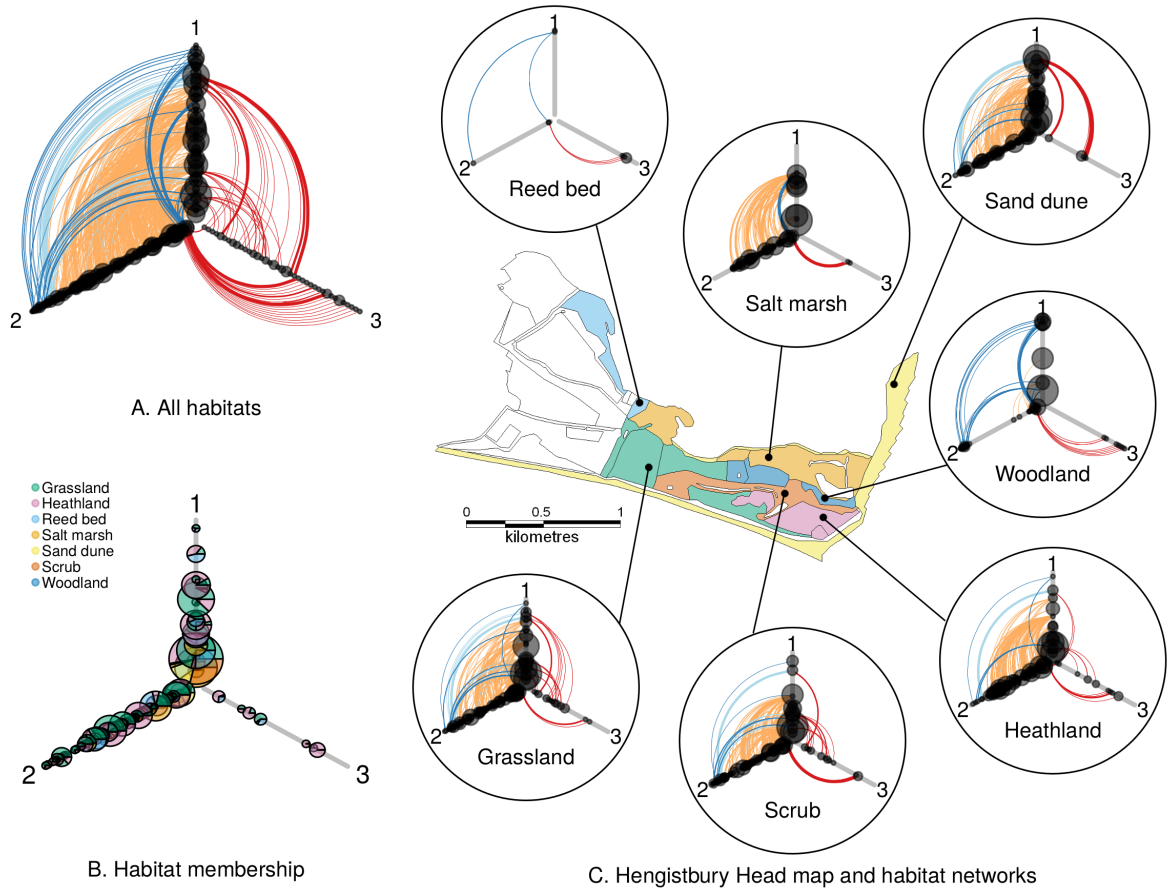


Figure 1: A) Landscape-scale network at Hengistbury Head (UK), B) habitat membership of species interacting in multiple habitats, and C) site map and ecological networks observed in each habitat of the site. Ecological networks are represented with hive plots (R package HiveR by Hanson, 2017): plants are drawn on axis 1, flower-visiting, seed-feeding and leaf-mining insects on axis 2, and parasitoids on axis 3. Nodes' size scales with species degree, edge colours correspond to the interaction type (orange: pollination, light blue: seed-feeding, dark blue: leaf-mining, red: parasiting), and wider edges indicate stronger interactions. As parasitised seed-feeders are destroyed before emergence, plants hosting parasitised seed-feeders are, here, directly linked to parasitoids. In B, only species involved in multiple habitats are plotted, with different sectors of the pie charts corresponding to different habitats. Larger sectors indicate that the species has been observed interacting more in the corresponding habitat. The Hengistbury Head map contains OS data ©Crown copyright and database right 2018.

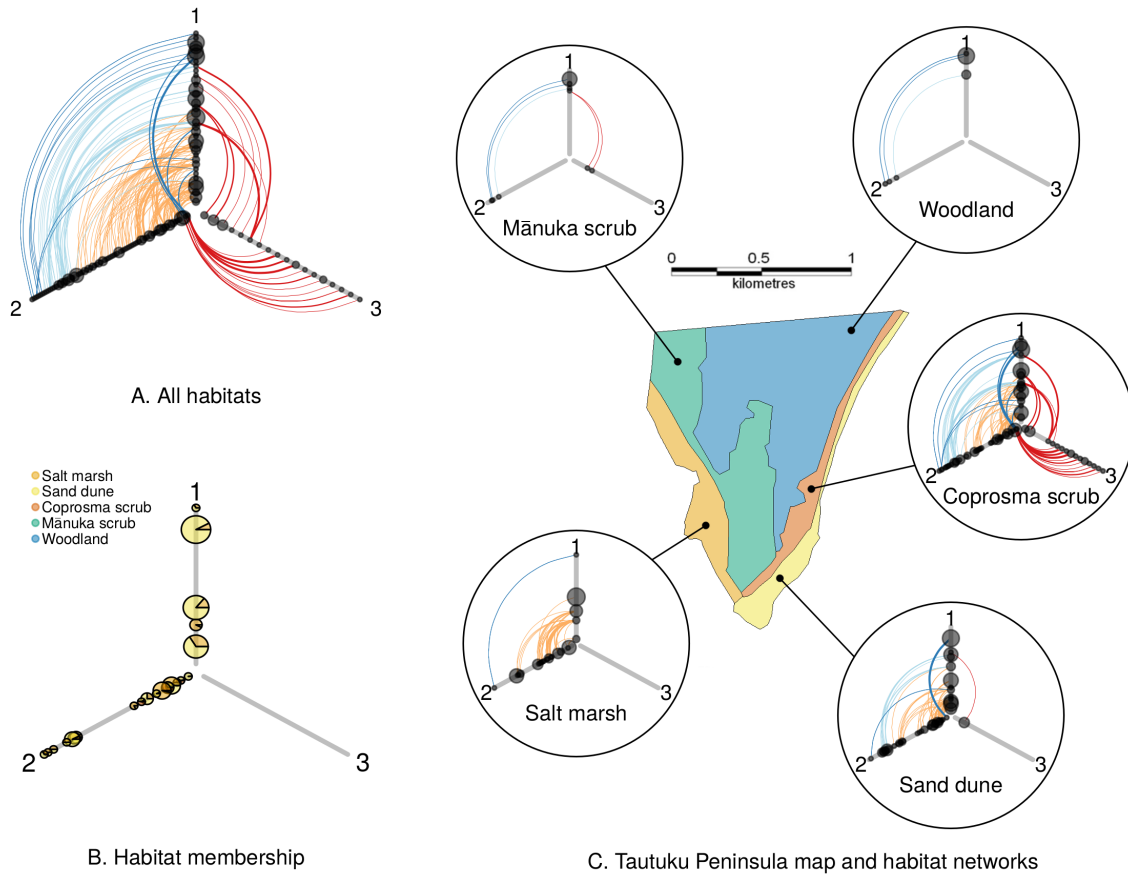


Figure 2: A) Landscape-scale network at Tautuku Peninsula (NZ), B) habitat membership of species interacting in multiple habitats, and C) site map and ecological networks observed in each habitat of the site. Ecological networks are represented with hive plots (R package HiveR by Hanson, 2017): plants are drawn on axis 1, flower-visiting, seed-feeding and leaf-mining insects on axis 2, and parasitoids on axis 3. Nodes' size scales with species degree, edge colours correspond to the interaction type (orange: pollination, light blue: seed-feeding, dark blue: leaf-mining, red: parasitism), and wider edges indicate stronger interactions. As parasitised seed-feeders are destroyed before emergence, plants hosting parasitised seed-feeders are, here, directly linked to parasitoids. In B, only species involved in multiple habitats are plotted, with different sectors of the pie charts corresponding to different habitats. Larger sectors indicate that the species has been observed interacting more in the corresponding habitat.

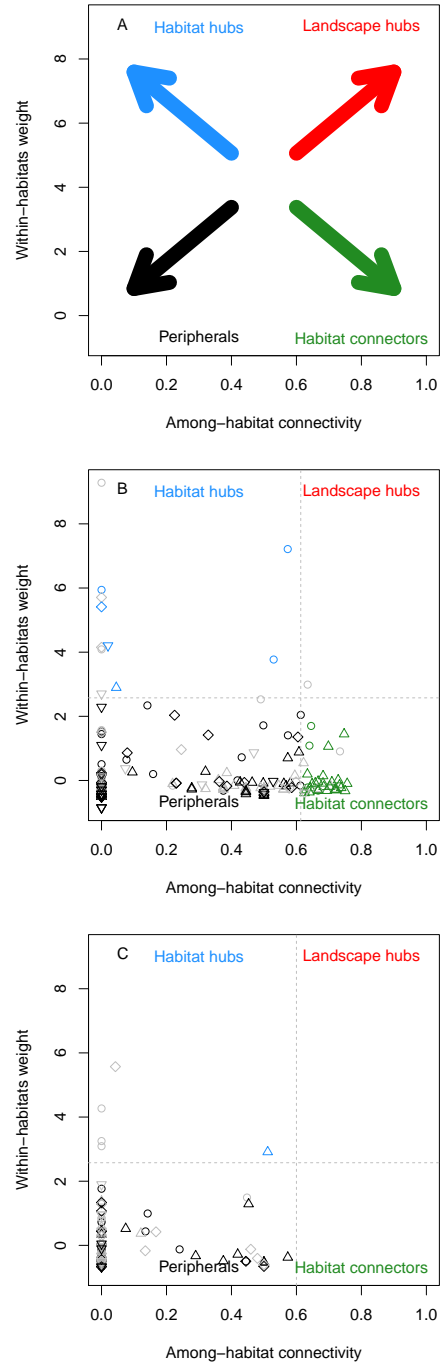


Figure 3: A) Distribution of species roles in the $\{z_i, c_i\}$ -plane. B-C) Species distribution in the $\{z_i, c_i\}$ -plane (within-habitat weight against among-habitat connectivity) according to the quantitative networks for B) Hengistbury Head (UK), and C) Tautuku Peninsula (NZ). Each symbol corresponds to a species: open circles for plants, upward triangles for flower visitors, diamonds for herbivores, downward triangles for parasitoids, and asterisks for insects involved in multiple interaction types. Symbol colour refers to the assigned landscape role (black: peripheral, green: habitat connector) if its position in the plane is significantly different than expected according to the null model (otherwise grey).

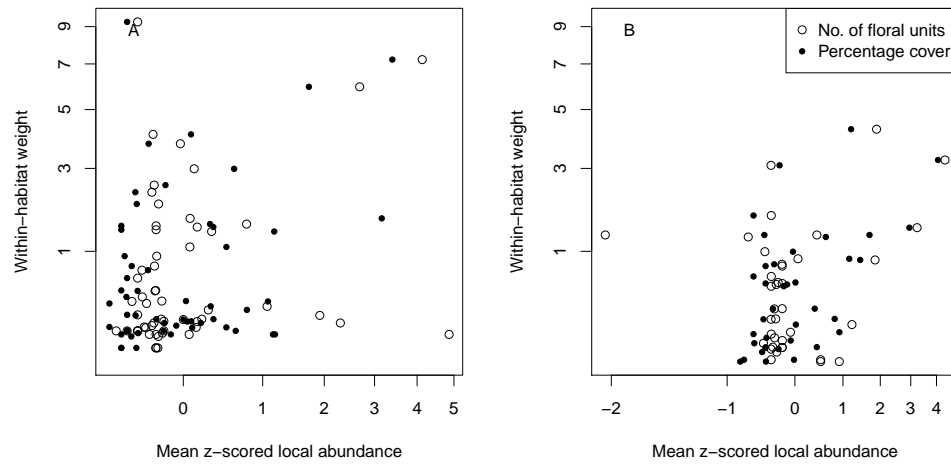


Figure 4: Within-habitat weight against the number of floral units (open circles) and against the percentage of cover (full circles) on a logarithmic scale for A) Hengistbury Head (UK), and B) Tautuku Peninsula (NZ). Each symbol corresponds to a plant species.

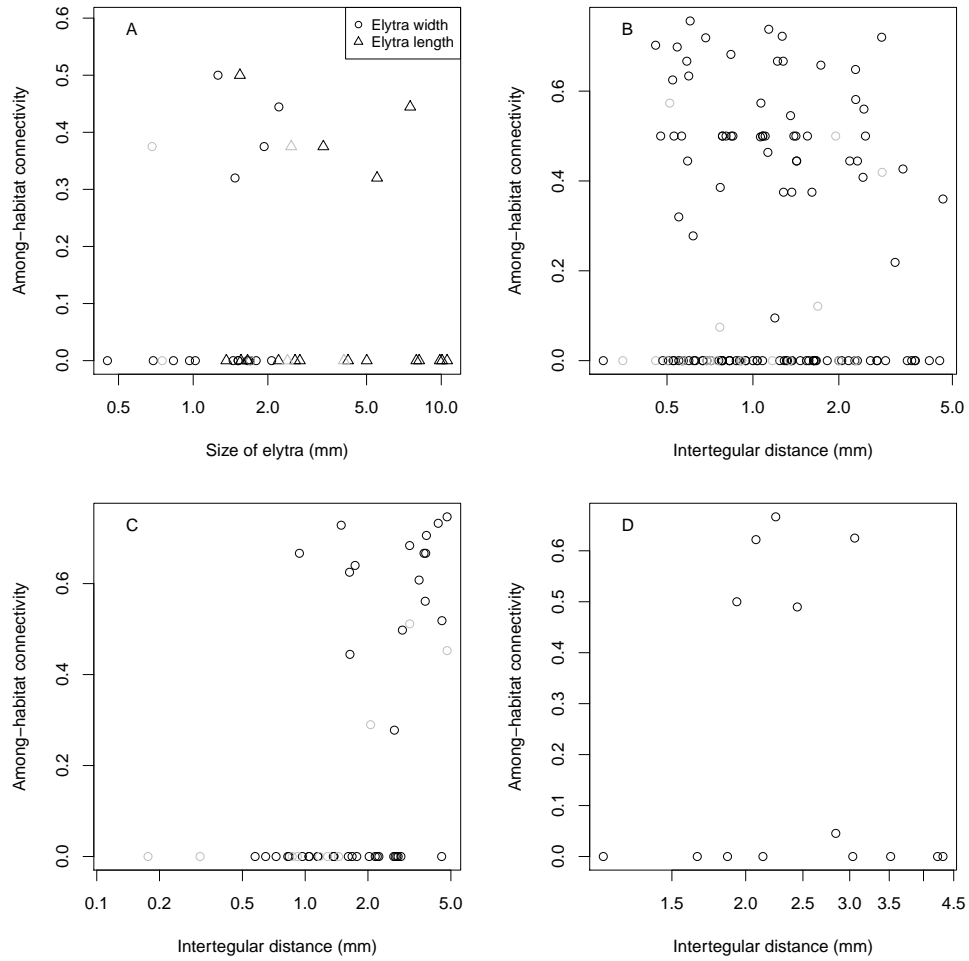


Figure 5: Among habitat connectivity of flower visitors versus their dispersal ability (measured as elytra size for Coleoptera or intertegular distance for the other orders): A) Coleoptera (open circle for the width of the elytra, and cross for its length), B) Diptera, C) Hymenoptera, and D) Lepidoptera. Each symbol corresponds to an insect species, and is displayed in grey when specific to Tautuku Peninsula (NZ).

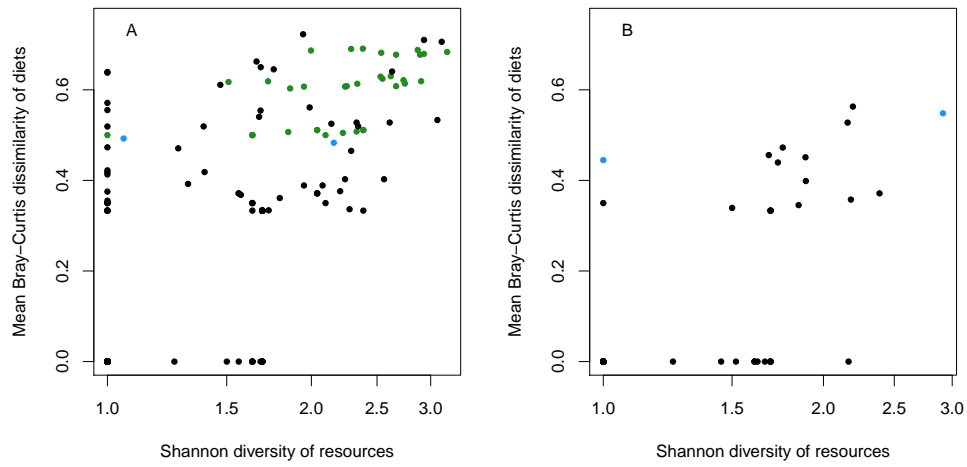


Figure 6: Mean dissimilarity of diets across habitats, calculated with Bray-Curtis dissimilarity, against the Shannon diversity of resources for insect species for A) Hengistbury Head (UK), and B) Tautuku Peninsula (NZ). Each symbol corresponds to an insect species, and its color matches its landscape role (black: peripheral, green: habitat connector) if its position in the plane is significantly different from expected according to the null model (otherwise grey).

Supplementary information from “Reshaping our understanding of
species’ roles in landscape-scale networks”

Talya D. Hackett, Alix M. C. Sauve, Nancy Davies, Daniel Montoya, Jason Tylianakis &
Jane Memmott

Appendix S1: Sampling protocols for the metaweb

Field sites

Fieldwork was based at two field sites, one in the United Kingdom (Hengisbury Head: $50^{\circ}4'59.67''\text{N}$ $1^{\circ}45'22.74''\text{W}$, 162 ha in size) and the other in New Zealand (Tautuku Peninsula: $46^{\circ}35'30.68''\text{S}$ $169^{\circ}25'39.46''\text{E}$, 225 ha in size). Both sites consisted of multiple habitats, the UK site was comprised of seven habitats: grassland, heathland, woodland, salt marsh, scrub, sand dune and reed bed; and the New Zealand site consisted of five habitats: *Coprosma* scrub, Mānuka scrub (*Leptospermum scoparium*), salt marsh, woodland and sand dune (Fig. 1 and 2 in the main text).

At both sites we selected two plots in each habitat, each plot delimiting an area equivalent to 5% of each habitat's area. At Hengistbury Head, each plot was sampled once a month from June-September in 2013; the 14 plots were therefore sampled four times in total. Each month we randomly chose one of the two plots in each habitat to sample first and then sampled the remaining one on the next visit. Tautuku Peninsula was sampled in the same manner five times from November 2014 to February 2015 (i.e. during the Austral Summer).

Network construction

Sampling plants

A 50 m transect, placed at a randomly selected start point and direction on each visit, was used to sample each plot for plants. Every 10 m we placed a 0.5 m^2 gridded quadrat on alternating sides of the transect, and within this, we identified all flowering plants to species and counted the number of floral units. To quantify the vegetation, we counted each time a flowering plant touched one of the 36 cross points (*CP*) of the gridded quadrat and assigned a vegetative cover measure of 1 to 4 (as in Gibson *et al.*, 2007). Category 1 plants were rare, only present one to a few times in the quadrat (1-2%), category 2 were present in high enough numbers to be seen easily (occupied $< 10\%$ of the quadrat area), category 3 could be seen throughout the quadrat ($< 50\%$ of the area) and category 4 were the most abundant ($> 50\%$ of the area). Grasses were identified collectively and given a 1-4 vegetative cover measurement, all other plants were identified to species and classified both with cross points and the 1-4 scale for confirmation to account for a plant occurring in a quadrat but not touching a cross point. Plants that were seen along the transect but not in a quadrat were recorded

as Category 1 plants (i.e. 1-2% of the area). We then calculated an overall percentage cover from these two measurements. Where there was a cross point, percentage cover was $CP/36 \times 100$, where we recorded only vegetative cover (e.g. grass), the middle percentage was taken (e.g. 1%, 7%, 35% and 75%). In 21 cases the plant did not touch a cross point, but the vegetative cover was greater than 1 (in 20 cases it was 2, in 1 case it was 3). In these cases, we substituted a minimum cross point value to satisfy the respective vegetative cover as a conservative estimate (e.g. 2.8% for a vegetative cover of 2 and 11.1% for 3).

Plant-pollinator network construction

Flower visitors were sampled by haphazard walking for 30 min in each plot in dry, warm conditions (at least 15°C), with a little or no wind, between 9:00 and 17:30. All insects seen on flowers were collected using a hand net, the interaction recorded and the insect identified to species by taxonomists (see acknowledgements for information concerning taxonomists).

Plant-herbivore-parasitoid network construction

We sampled two guilds of herbivores - leaf miners and seed feeders, along with the plants they fed on, and the parasitoids that attacked them. Both groups were sampled from a 1 m² quadrat placed every 10 m along the transect line in each plot, searching up to 2 m in height for taller vegetation. All insects were identified to species by taxonomists.

We collected the leaves containing leaf miner larvae and identified leaf miners from the leaf mine pattern (Pitkin *et al.*, 2007; Dickerson, 2007). Leaf miners were reared individually and checked every 2-3 days for emergence of either leaf miner adults or parasitoids.

Finally, we collected up to 50 seeds and reared insects from 9 species of plants on Hengistbury Head: *Cirsium arvense*, *Cirsium vulgare*, *Cytisus scoparius*, *Dipsacus fullonum*, *Lotus corniculatus*, *Rubus fruticosus*, *Trifolium pratense*, *Trifolium repens* and *Ulex europeus*; these species being selected as the most likely to host seed feeders from previous studies in the UK (Pocock *et al.*, 2012). We followed the same protocol in Tautuku Peninsula, collecting from 10 species which had seed heads similar to those of plants collected in the UK: *Centaureum erythraea*, *Chrysanthemum leucanthemum*, *Cirsium arvense*, *Coprosma lucida*, *Gaultheria antipoda*, *Lupinus arboreus*, *Microtris uniflora*, *Plantago lanceolata*, *Pseudognaphalium lutealbum* and *Veronica salicifolia*. At both sites,

seeds were collected from within 10 m from the transect line and where possible they were collected from multiple plants at multiple locations along the transect line. Seed herbivores were reared collectively until adult herbivores or parasitoids emerged.

Appendix S2: Definition of species roles at the landscape scale

In a given habitat, network ecologists depict networks of interactions as ordered pairs $G = (V, E)$ where:

- V is a set of species;
- E is the set of interactions occurring between species. Hence, E is a subset of all possible interactions (i.e. $E \subseteq V \times V$).

Usually, an adjacency matrix A is defined such that non-zero element A_{ij} corresponds to the interaction between species i and j ($\{i, j\} \in [1, |V|]$, where $|V|$ denotes the size of V , i.e. the number of species).

In a mosaic of habitats, networks of ecological interactions can be described as having several ‘layers’, each corresponding to a given habitat, and multilayer networks provide a framework to describe such networks (Pilosof *et al.*, 2017). We denote $G_M = (V_M, E_M, V, L)$ the quadruplet describing a landscape scale network:

- L is the set of habitats (‘layers’).
- V_M the set of {species, habitat}-couples of G_M that encodes the occurrence of each species within the set of habitats that constitute the landscape (i.e. $V_M = \{(u, l), u \in V, l \in L\} \subseteq V \times L$).
- E_M lists two types of edges: the interactions that occur between species within each habitat, also named ‘intra-layer edges’ ($E_{intra} = \{((u, \alpha), (v, \beta)) \in E_M | \alpha = \beta\}$), and the links between habitats that are used to signify all occurrences of the same species across habitats, namely the ‘inter-layer edges’ ($E_{inter} = \{((u, \alpha), (v, \beta)) \in E_M | u = v\}$).

The intra-layer edges that depict interactions among species within each habitat are represented in an adjacency tensor B . This tensor is actually an array of matrices, whereby each matrix describes the interactions that occur among species in a given habitat. Thus, its size is $|V| \times |V| \times |L|$, where $|V|$ and $|L|$ denote the number of species and habitats respectively. Each element B_{ijh} corresponds to the interaction between species i and species j in habitat h ($i \in V$, $j \in V$, and $h \in L$). It is equal to 1 if species i and species j interact in habitat h , and 0 otherwise.

We then apply weights to these binary links by using the function $q : E_{intra} \mapsto \mathbb{R}^+$ that associates a weight to each interaction (for instance, an interaction frequency), such that $q(B_{ijh})$ is the weight of the interaction between species i and species j interact in habitat h . Thus, all our network analyses involve weighted networks.

Defining species roles in the landscape

We are interested in identifying functionally important species within a mosaic of habitats in terms of whether they play the role of hubs or connectors between habitats. In this context, we primarily aim to understand how the different habitats characterising one landscape are connected together by species.

We define four broad categories: **habitat hubs** are important species (due to multiple and/or strong links) in a specific habitat, **landscape hubs** are important species in multiple habitats, **habitat connectors** are found more equally interacting in multiple habitats but are involved in fewer interactions than hubs, and **peripheral species** are found predominantly in one habitat and are involved in fewer interactions than hubs.

Our classification is actually inspired by Guimera and Amaral’s approach which requires the calculation of two indices: the within-module degree and the participation coefficient (Guimera & Amaral, 2005). However, we adapt their framework to apply to landscape-scale networks; we define groups as habitats instead of clusters of interactions (‘module’). Consequently, we take into account that species belong to multiple habitats with various degrees of membership.

To classify species, we characterise each species’ relative importance within habitats with respect to their habitat generalism - i.e. how evenly its interactions are distributed among habitats. This is captured by the relative values of two indices which we define below (emphasised in bold).

The local within-habitat weight z_{ih} is the z-score of species i ’s weight in habitat h , and it measures how strongly it is connected in the focal habitat:

$$z_{ih} = \frac{(k_{ih} - k_h)}{\sigma_{j \in V_h}(k_{jh})} \quad (1)$$

where $k_{ih} = \sum_j q(B_{ijh})$ is the weight of species i in habitat h , k_h is the average weight of species occurring within habitat h , and $\sigma_{j \in V_h}(k_{jh})$ the standard deviation of species weight in habitat h (V_h is the set of species present in habitat h).

We define the **within-habitat weight** z_i of species i as the weighted-arithmetic mean of its local within-habitat weights z_{ih} :

$$z_i = \sum_h \beta_{ih} z_{ih} \quad (2)$$

where β_{ih} is the belonging coefficient of species i to habitat h which is the proportion of species i 's interactions that occur within habitat h . Hence, β_{ih} is the ratio of the weight of species i 's interactions within habitat h over the weight of all its interactions: $\beta_{ih} = \frac{\sum_j q(B_{ijh})}{\sum_{j,k} q(B_{ijk})}$.

The **among-habitat connectivity** c_i (defined as the 'participation coefficient' by Guimera & Amaral, 2005) measures how evenly distributed the interactions of a given species are in the landscape:

$$c_i = 1 - \sum_h \beta_{ih}^2 \quad (3)$$

c_i tends towards 1 if interactions are distributed evenly among the habitats, whereas it tends towards 0 if interactions occur mainly in a single habitat.

These indices can be applied to qualitative networks as well by replacing weights with species' degrees.

The four defined species roles can be demarcated in the $\{z_i, c_i\}$ -space: peripheral species have a low z_i and a low c_i , habitat connectors have a low z_i and a high c_i , habitat hubs have a high z_i and a low c_i and landscape hubs have a high z_i and a high c_i (Fig. S2.1).

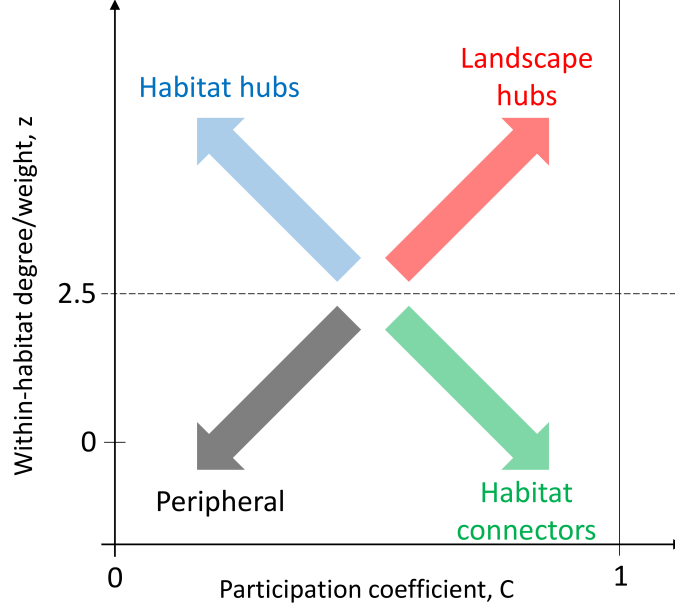


Figure S2.1: Distribution of species roles in the $\{z_i, c_i\}$ -space.

Landscape roles based on species' $\{z_i, c_i\}$ -coordinates and their links distribution

While species roles can be identified based on their $\{z_i, c_i\}$ -coordinates, definitions for ‘low’ or a ‘high’ values for the within-habitat weight or the among-habitat connectivity are less precise. However, following Guimera & Amaral (2005), we can identify thresholds for z_i and c_i to discriminate each role. Although Guimera & Amaral (2005) identify seven network roles (Fig. S2.3B), we use the simpler classification of Olesen *et al.* (2007), and define one threshold value for z_i and one for c_i (Fig. S2.1 and Fig. S2.3A).

A threshold for the within-habitat weight

As the within-habitat weight z_i is based on standard scores, the natural threshold above which z_i is significantly higher than for the rest of the community is 2.576, the critical value for a significance level $\alpha = 0.005$, hence fixing the chance of type I error.

A threshold for the among-habitat connectivity

Among-habitat connectivity c_i is based on the distribution of one species' interactions across habitats, and requires the calculation of its belonging coefficient β_{ih} within each habitat h . Following

Guimera & Amaral (2005), we define connectors as species with highest belonging coefficient below 60%. Thus, connector species must have less than 60% their interactions occurring within the same habitat.

To define a threshold for c_i , we calculated the highest c_i value corresponding to a species that has up to 60% of its interactions occurring within the same habitat. If species i has its greatest belonging coefficient $\beta_{i1} = 60\%$, its among-habitat connectivity is:

$$c_i = 1 - \beta_{i1}^2 - \sum_{h \neq 1} \beta_{ih}^2 = 0.64 - \sum_{h \neq 1} \beta_{ih}^2 \quad (4)$$

Hence, c_i depends both on the number of habitats in which species i occurs, denoted as n_i , and its belonging coefficients in those various habitats. c_i is maximised if the interactions happening in habitats other than $h = 1$ are equally distributed in the $n_i - 1$ remaining habitats so that

$$c_i \leq 1 - \beta_{i1}^2 - \sum_{h \neq 1} \left(\frac{1 - \beta_{i1}}{n_i - 1} \right)^2 = 1 - \beta_{i1}^2 - \frac{(1 - \beta_{i1})^2}{n_i - 1} \quad (5)$$

The upper-bound of c_i depends on n_i , increasing asymptotically when the number of habitats to which species i belongs gets higher until reaching a plateau (Fig. S2.2).

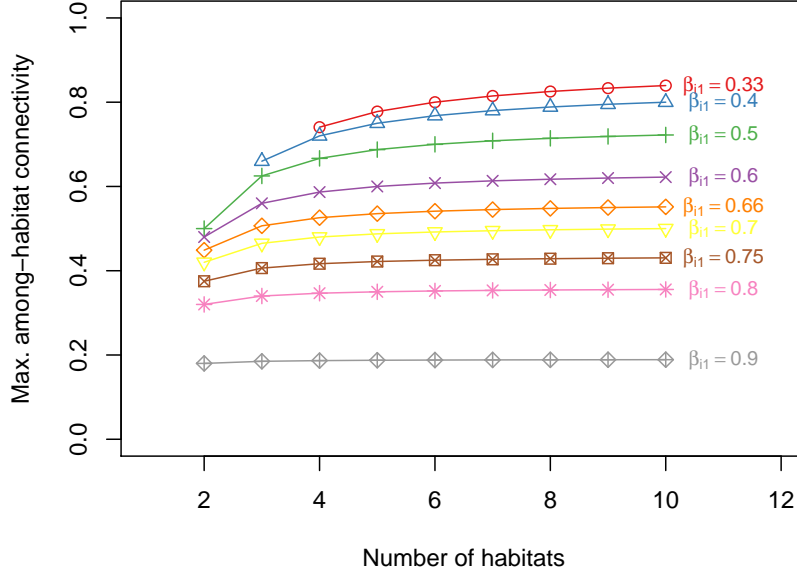


Figure S2.2: The maximum among-habitat connectivity $\max(c_i)$ against the number of habitats to which species i belongs. $\max(c_i)$ is displayed for different values of highest belonging coefficient (from top to bottom: $\beta_{i1} = \{0.33, 0.4, 0.5, 0.6, 0.66, 0.7, 0.8, 0.9\}$).

Instead of defining a threshold for each species in the landscape, we used $1 - \beta_{i1}^2 - \frac{(1-\beta_{i1})^2}{|L|-1} = 0.64 - \frac{0.16}{|L|-1}$ as a threshold ($|L|$ being the size of the set of layers, i.e., the number of habitats).

Thus, we classify species as follows (Fig. S2.3A):

- Peripheral species have $z_i < 2.576$, and $c_i \leq 0.64 - 0.16/(|L| - 1)$.
- Habitat connectors have $z_i < 2.576$, and $c_i > 0.64 - 0.16/(|L| - 1)$.
- Habitat hubs have $z_i \geq 2.576$, and $c_i \leq 0.64 - 0.16/(|L| - 1)$.
- Landscape hubs have $z_i \geq 2.576$, and $c_i > 0.64 - 0.16/(|L| - 1)$.

More subtle landscape roles may be identified with the same rationale (Guimera & Amaral, 2005, Fig. S2.3B):

- Ultra-peripheral species which are found in a single habitat: $z_i < 2.576$, and $c_i = 0$.
- Peripheral species which have more than 60% their links within the same habitat: $z_i < 2.576$, and $c_i \leq 0.64 - \frac{0.16}{|L|-1}$.

- Non-hub habitat-connectors which most have more than one third of their links within the same habitat: $z_i < 2.576$, and $0.64 - \frac{0.16}{|L|-1} < c_i \leq 8/9 - \frac{4/9}{|L|-1}$.
- Non-hub kinless (meaning they are not particularly bound to a given habitat) habitat-connectors which have a very high habitat generalism: $z_i < 2.576$, and $c_i > 8/9 - \frac{4/9}{|L|-1}$.
- Most provincial habitat-hubs have at least 80% of their links within the same habitat: $z_i \geq 2.576$, and $c_i \leq 0.36 - \frac{0.04}{|L|-1}$.
- Habitat-connector hubs which most have at least 50% of their links within the same habitat: $z_i \geq 2.576$, and $0.36 - \frac{0.04}{|L|-1} < c_i \leq 0.75 - \frac{0.25}{|L|-1}$.
- Kinless hubs which are highly habitat generalists: $z_i \geq 2.576$, and $c_i > 0.75 - \frac{0.25}{|L|-1}$.

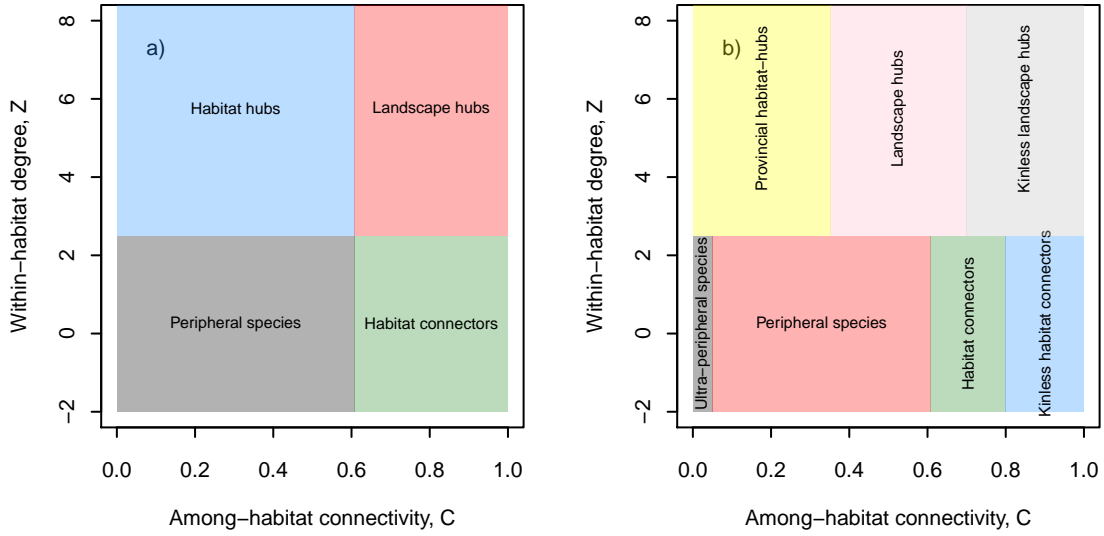


Figure S2.3: Landscape roles' and their regions in $\{z_i, c_i\}$ -space: A) for the basic classification, B) for subtle landscape roles.

For landscapes with a small number of habitats (e.g. < 10), we recommend calculating the corresponding c_i -threshold following our formula. However, for landscape settings involving a large number of habitat types, or habitat patches, asymptotic values of $\max(c_i)$ should be used.

Appendix S3: Dissimilarity of insect diets across habitats

Because species occur in multiple habitats, species could rely on different resources in the different habitats. Using the framework of Poisot *et al.* (2012), we investigated how species diet varies over the landscape. For each insect species, we compared the diet of the focal species within each habitat with its aggregated interactions at the landscape scale using a dissimilarity metric (Bray-Curtis dissimilarity). Then, we calculated the mean dissimilarity of diet for each species, this reflecting how dissimilar the foraged resources tend to be. The dissimilarity metric varies between 0 for similar diets and 1 for completely dissimilar diets. A high dissimilarity of diets indicates an insect species that feeds on different species in each habitat where it is found. We found that the more generalist an insect species is, in terms of Shannon diversity of resources, the more likely it is to feed on a different set of resources in each habitat where it is found (Fig. 4 in the main text). However, this result relies on the study of mean dissimilarities of diet and thus does not tell us how variable the trophic environment of a given species might be (Fig. S3.1). We verified the robustness of this relationship when considering each habitat separately for each species.

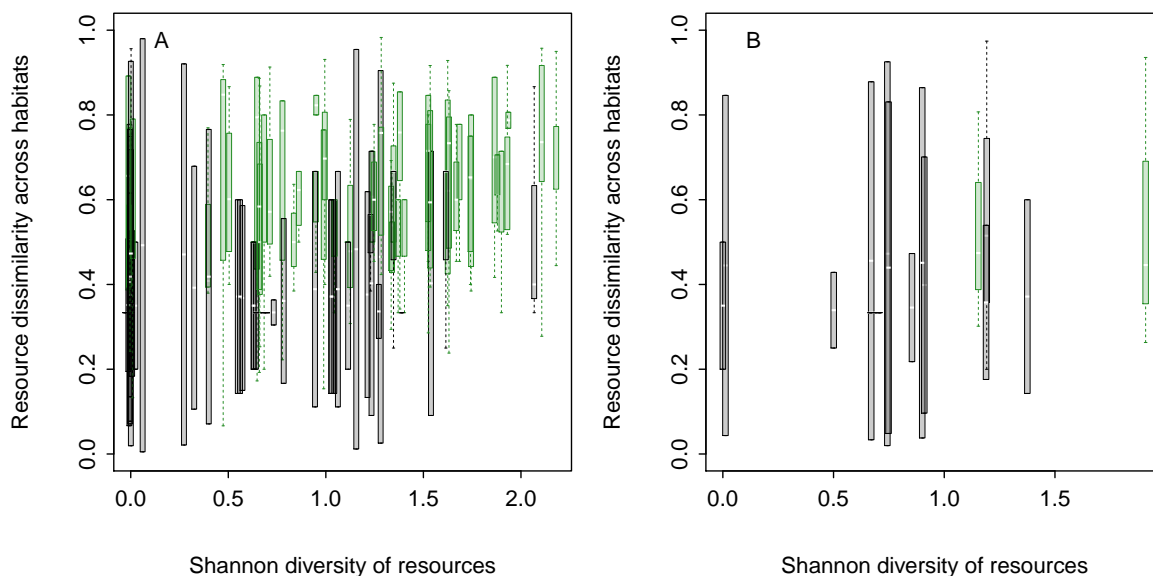


Figure S3.1: Resource dissimilarity across habitats in A) Hengistbury Head and B) Tautuku peninsula as a function of the Shannon diversity of resources for insect species. Each boxplot corresponds to a species and the colour refers to its landscape role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub).

We tested whether species' diversity of resources predicts the resource dissimilarity across habi-

tats using linear mixed models (using R package *lme4* by Bates *et al.*, 2014). As species identity and habitat may influence the resource dissimilarity of species across habitats, we considered models with random effects on the intercept. We selected the best model by comparing the *AIC* of models without random effect and also with species, habitat, or both as random effects on the intercept.

Neither the habitat nor the species identity influences the resource dissimilarity across habitats in both sites. In Hengistbury Head, insects with the widest range of resources tend to change diet from one habitat to another with an increase of ~ 0.11 of resource dissimilarity per additional resource in the complete diet ($df = 325$, $p < 0.001$), while this relationship is not significant for Tautuku Peninsula (~ 0.09 , $df = 37$, $p = 0.35$ for Tautuku peninsula).

Appendix S4: Details of the null model

Staniczenko *et al.* (2017) found that parasitoids’ foraging preferences may change between habitat types independently of the relative abundances of their resources. This could be also the case for other groups of insects and we hypothesise that changes in foraging behaviour could determine to species roles. To test this hypothesis, we generated landscape-scale networks which preserve the observed distribution of plant species (see plant survey), and assumed that the foraging behaviour of insect species is only driven by their resource relative abundance in each habitat. For each site, we generated these networks as follows.

Since the plant community is an important factor to delimit habitat types, we started with the raw data on plant species in each habitat as recorded during the vegetation survey, this includes the plants that have no recorded interactions with other species (cf. the corresponding section in ‘Material and methods’, Appendix S1). We proceeded by trophic level, from the lowest (i.e. pollinators, leaf-miners and seed-feeding insects) to the highest (i.e. parasitoids), and distributed the observed number of interaction events observed for each species assuming the interaction probability to be proportional to resource abundance.

- Step 1: For the insects feeding on plants, the probability they interact with a given plant of their diet is proportional to the plant abundance. We used the percentage of cover when distributing the leaf-miners interactions, and the number of floral units for pollinators and seed-feeding insects.
- Step 2: Similarly, parasitoids pick their hosts in the landscape (species and location) with a probability proportional to the number of individuals resulting from step 1.

Throughout this process, the potential interactions are the same as observed over the whole landscape. Thus, we preserved the overall structure of the network.

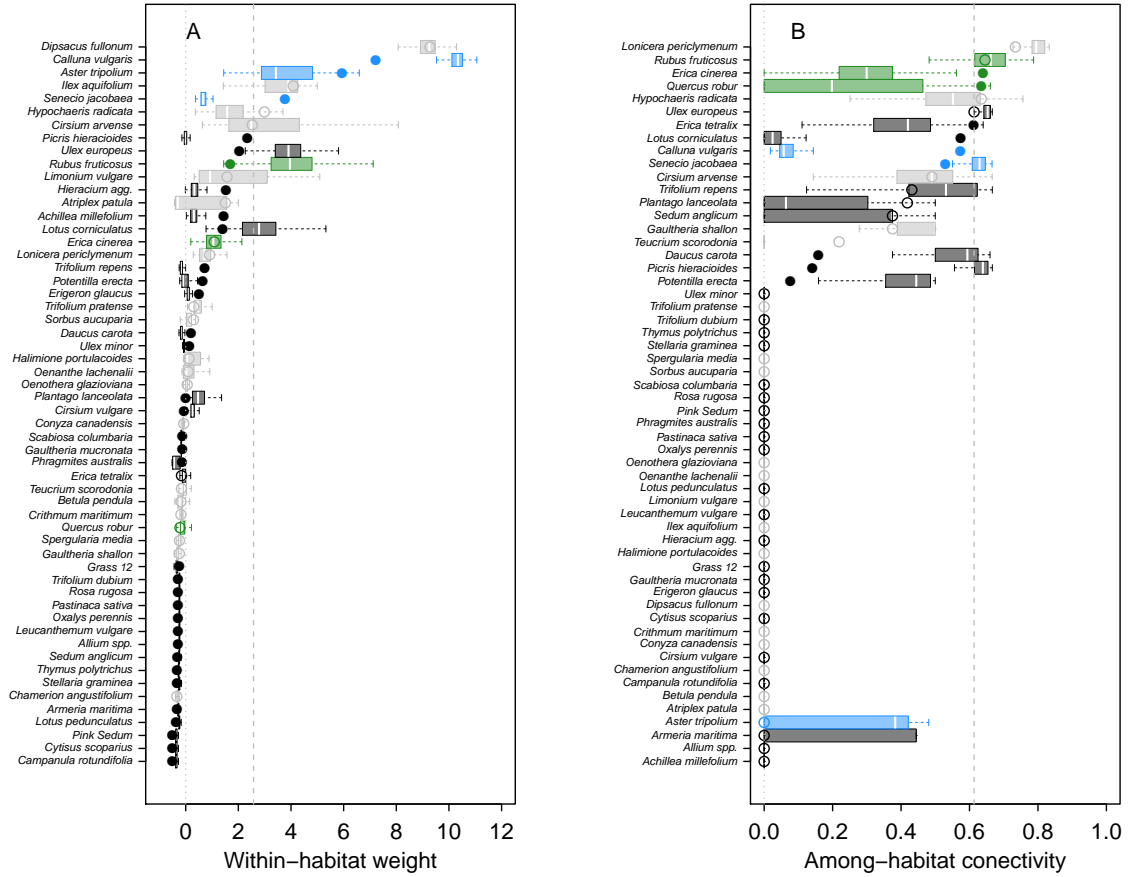


Figure S4.1: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of all plant species in Hengistbury Head. Plant species are ranked by descending observed values and the expected values for each are represented as boxplots. Observed values are represented by an open circle if not different than expected from the null model, and with a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the assigned species role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected (otherwise the colour grey is used).

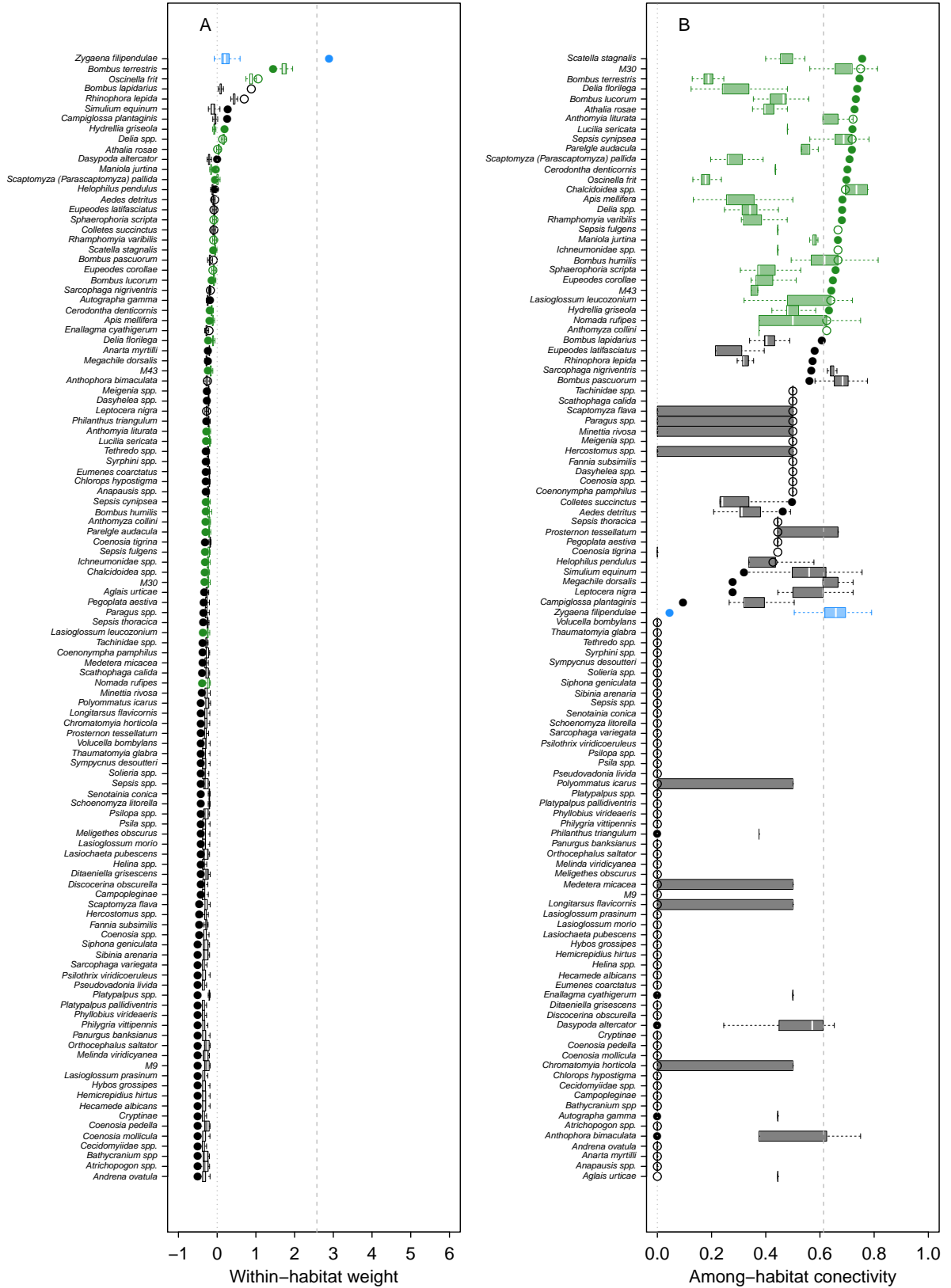


Figure S4.2: (On previous page) A) Within-habitat weight z_i and B) among-habitat connectivity c_i of flower visiting species in Hengistbury Head. Insect species are ranked by descending observed values, and the expected values for each are represented as boxplots. Observed values are represented by an open circle if not different than expected from the null model, and with a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the assigned species role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected (otherwise the colour grey is used). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are shown.

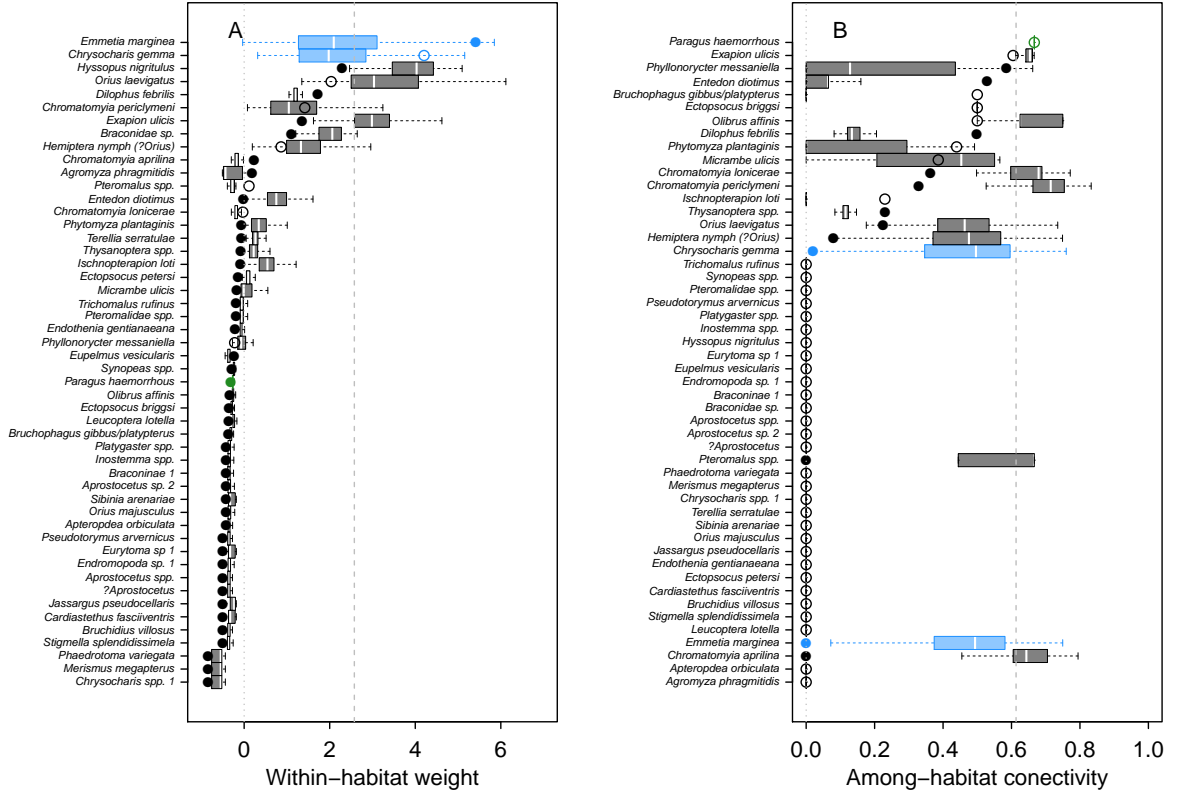


Figure S4.3: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of other insect species in Hengistbury Head (leaf-miners, seed-feeding insects, parasitoids). Insect species are ranked by descending observed values, and the expected values for each are represented as boxplots. Observed values are represented by an open circle if not different than expected from the null model, and with a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the assigned species role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected (otherwise the colour grey is used). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are shown.

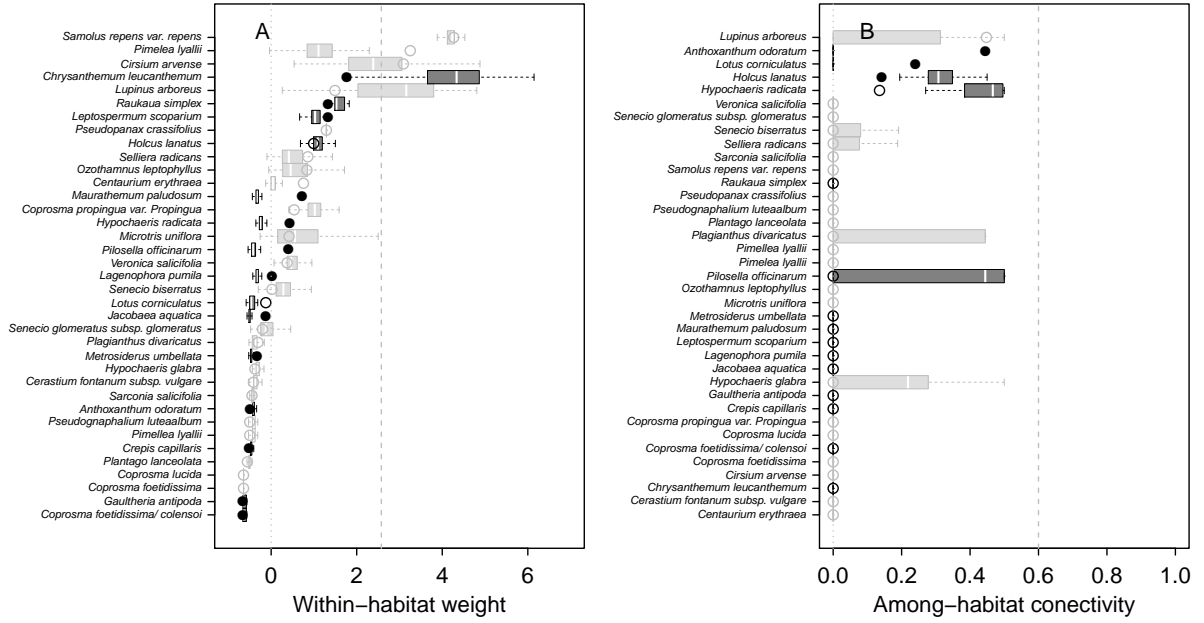


Figure S4.4: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of all plant species in Tautuku Peninsula. Plant species are ranked by descending observed values, and the expected values for each are represented as boxplots. Observed values are represented by an open circle if not different than expected from the null model, and with a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the assigned species role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected (otherwise the colour grey is used).

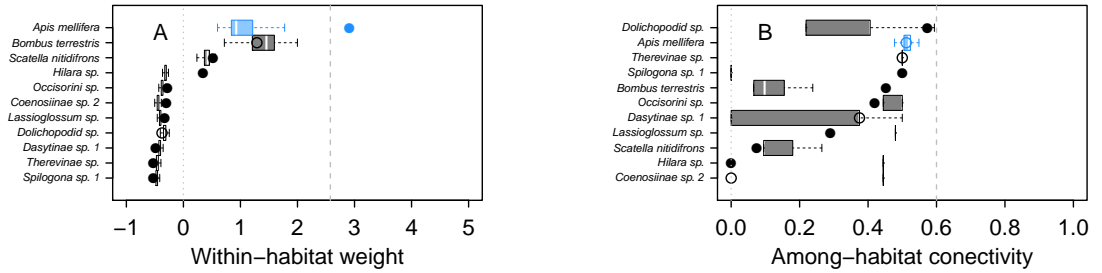


Figure S4.5: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of flower visiting species in Tautuku Peninsula. Insect species are ranked by descending observed values, and the expected values for each are represented as boxplots. Observed values are represented by an open circle if not different than expected from the null model, and with a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the assigned species role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected (otherwise the colour grey is used). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are shown.

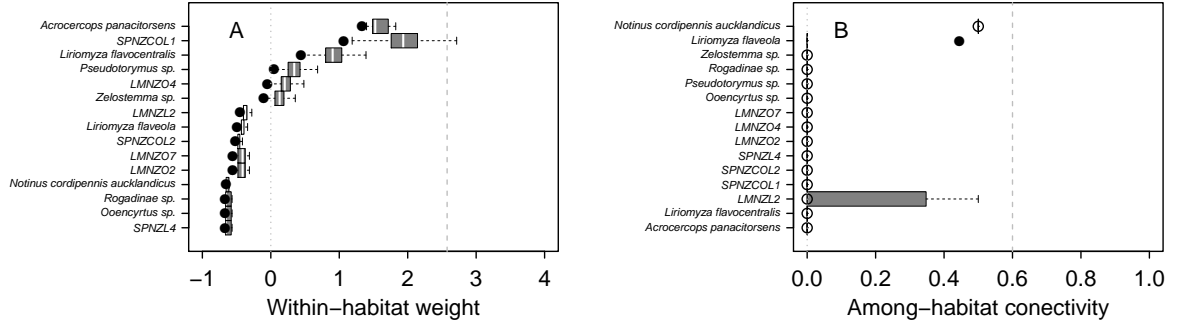


Figure S4.6: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of other insect species in Tautuku Peninsula (leaf-miners, seed-feeding insects, parasitoids). Insect species are ranked by descending observed values, and the expected values for each are represented as boxplots. Observed values are represented by an open circle if not different than expected from the null model, and with a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the assigned species role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected (otherwise the colour grey is used). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are shown.

Appendix S5 Network descriptors of the landscape scale food web

Habitat	Interaction type	Number of plant species	Number of insect species	Size of the lower guild	Size of the upper guild	Number of interaction events	Connectance
Grassland	FV	20	86	20	86	356	0.091
	SF	7	11	7	11	24	0.143
	SFP	5	11	5	11	17	0.218
	LM	2	8	5	8	43	0.2
	LMP	0	4	2	2	2	0.5
Heathland	FV	12	85	12	85	434	0.11
	SF	2	3	2	3	23	0.5
	SFP	2	5	2	5	5	0.5
	LM	5	5	2	5	28	0.5
	LMP	0	6	1	5	8	1
Reed bed	FV	-	-	-	-	-	-
	SF	-	-	-	-	-	-
	SFP	-	-	-	-	-	-
	LM	2	3	2	3	10	0.5
	LMP	0	5	2	3	3	0.5
Salt marsh	FV	9	70	9	70	202	0.149
	SF	-	-	-	-	-	-
	SFP	-	-	-	-	-	-
	LM	1	2	1	2	84	1
	LMP	0	4	2	2	10	0.5
Sand dune	FV	23	79	23	79	329	0.079
	SF	3	7	3	7	66	0.429
	SFP	1	4	1	4	58	1
	LM	5	5	5	5	9	0.2
	LMP	-	-	-	-	-	-
Scrub	FV	12	73	12	73	302	0.135
	SF	4	9	4	9	31	0.306
	SFP	4	9	4	9	22	0.278
	LM	4	10	4	10	40	0.25
	LMP	0	3	1	2	10	1
Woodland	FV	3	5	3	5	5	0.333
	SF	-	-	-	-	-	-
	SFP	-	-	-	-	-	-
	LM	7	21	7	21	107	0.15
	LMP	0	14	7	7	8	0.163

Table S5.1: Network descriptors in each habitat of Hengistbury Head, and for each type of network. Interaction types are abbreviated as follows: *FV* for plant-flower visitor interactions, *SF* for plant-seed feeder interactions, *SFP* for plant-herbivore-parasitoid interactions (simplified to the plant-parasitoid link, see methods in the main text for further explanation), *LM* for plant-leaf miner interactions, and *LMP* for leaf miner-parasitoid interactions.

Habitat	Interaction type	Number of plant species	Number of insect species	Size of the lower guild	Size of the upper guild	Number of interaction events	Connectance
Salt marsh	FV	4	20	4	20	118	0.325
	SF	-	-	-	-	-	-
	SFP	-	-	-	-	-	-
	LM	1	1	1	1	1	1
	LMP	-	-	-	-	-	-
Sand dune	FV	9	23	9	23	103	0.179
	SF	3	7	3	7	14	0.333
	SFP	1	1	1	1	1	1
	LM	2	2	2	2	7	0.5
	LMP	-	-	-	-	-	-
<i>Coprosma</i> scrub	FV	10	23	10	23	126	0.1609
	SF	5	11	5	11	57	0.309
	SFP	3	4	3	4	28	0.417
	LM	6	6	6	6	86	0.222
	LMP	0	14	3	11	22	0.364
Scrub Mānuka	FV	-	-	-	-	-	-
	SF	1	1	1	1	1	1
	SFP	1	2	1	2	2	1
	LM	2	2	2	2	5	0.5
	LMP	-	-	-	-	-	-
Woodland	FV	-	-	-	-	-	-
	SF	1	1	1	1	1	1
	SFP	-	-	-	-	-	-
	LM	2	2	2	2	3	0.5
	LMP	-	-	-	-	-	-

Table S5.2: Network descriptors in each habitat of Tautuku Peninsula, and for each type of network. Interaction types are abbreviated as follows: *FV* for plant-flower visitor interactions, *SF* for plant-seed feeder interactions, *SFP* for plant-herbivore-parasitoid interactions (simplified to the plant-parasitoid link, see methods in the main text for further explanation), *LM* for plant-leaf miner interactions, and *LMP* for leaf miner-parasitoid interactions.

Appendix S6: Species distribution in landscape-scale network roles

	Peripherals	Habitat hubs	Habitat connectors	Landscape hubs	Total
Plants	46	5	4	1	56
Flower visitors	183	1	33	0	217
Herbivores	52	3	0	0	55
Parasitoids	36	2	1	0	39
Insects foraging via > 1 interaction type	2	0	1	0	3
Total	319	11	39	1	370

Table S6.1: Contingency table describing the number of the various species groups within each landscape-scale network role in Hengistbury Head.

	Peripherals	Habitat hubs	Habitat connectors	Landscape hubs	Total
Plants	34	3	0	0	37
Flower visitors	52	1	0	0	53
Herbivores	24	1	0	0	25
Parasitoids	18	0	0	0	18
Total	128	5	0	0	133

Table S6.2: Contingency table describing the number of the various species groups within each landscape-scale network role in Tautuku Peninsula.

Hengistbury Head				Tautku Peninsula		
	Order/Family	Species	Interaction type(s)	Order/Family	Species	Interaction type(s)
Plants	<i>Asteraceae</i>	<i>Aster tripolium</i>	FV, LM	<i>Asteraceae</i>	<i>Cirsium arvense</i>	FV, SF, P
	<i>Ericaceae</i>	<i>Calluna vulgaris</i>	FV	<i>Thymelaeaceae</i>	<i>Pimelea lyallii</i>	FV
	<i>Caprifoliaceae</i>	<i>Dipsacus fullonum</i>	SF, P	<i>Primulaceae</i>	<i>Samolus repens</i> <i>var. repense</i>	FV
	<i>Aquifoliaceae</i>	<i>Ilex aquifolium</i>	LM			
	<i>Asteraceae</i>	<i>Senecio jacobea</i>	FV, LM			
Habitat hubs	<i>Hymenoptera/Braconidae</i>	<i>Apanteles maritimus</i>	P	<i>Hymenoptera/Apidae</i>	<i>Apis mellifera</i>	FV
	<i>Lepidoptera/Bucculatricidae</i>	<i>Bucculatrix maritima</i>	LM, P	<i>Diptera/Agromyzidae</i>	<i>Cerodontha angustipennis</i>	LM, P
	<i>Hymenoptera/Chalcidoidea</i>	<i>Chrysocharis gemma</i>	P			
	<i>Lepidoptera/Tischeriidae</i>	<i>Emmetia marginea</i>	LM, P			
	<i>Diptera/Agromyzidae</i>	<i>Phytomyza ilicis</i>	LM, P			
Insects	<i>Lepidoptera/Zygaenidae</i>	<i>Zygaena filipendulae</i>	FV			
	<i>Asteraceae</i>	<i>Hypochaeris radicata</i>	FV, LM			
Landscape hubs						

Table S6.3: List of plant and insect species identified as habitat and landscape hubs in Hengistbury Head and Tautuku Peninsula. Interaction types are abbreviated as follows: *FV* for plant-flower visitor interactions, *LM* for leaf mining interactions, *P* for host-parasitoid interactions, and *SF* for seed-feeding interactions. As parasitoids of seed-feeders destroy their hosts before emergence, plants hosting parasitised seed-feeders are, here, directly linked to parasitoids.

Appendix S7: Context dependency of the relationship between plant species' abundance and their within-habitat weight

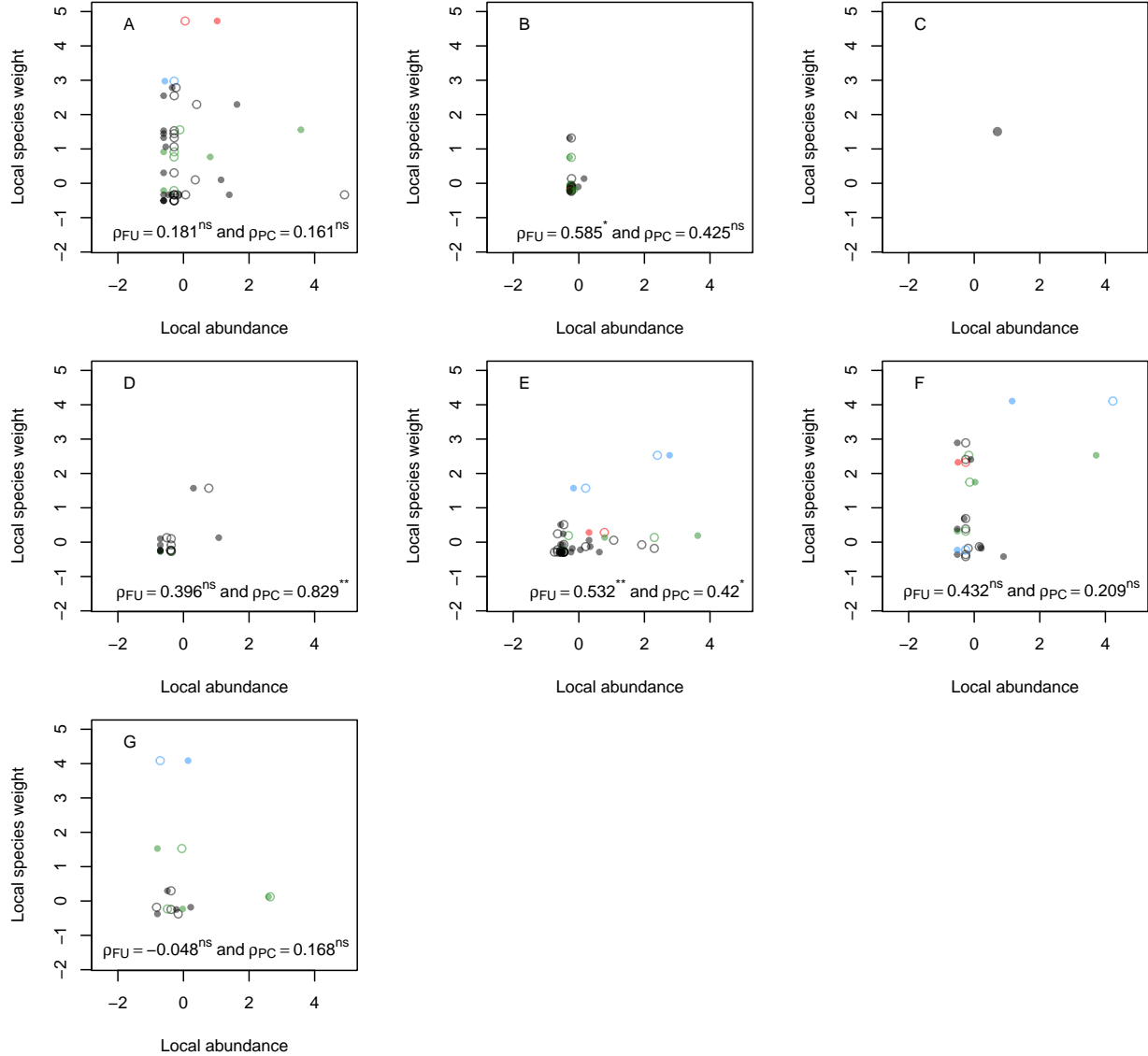


Figure S7.1: Within-habitat weight against the number of floral units (open circles) and against the percentage of cover (full circles) of plant species for Hengistbury Head. Each symbol corresponds to a plant species, and is coloured according to their role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub). Estimated correlation coefficients (ρ_{FU} and ρ_{PC} for abundances estimated based on floral units and percentage cover respectively) between log-transformed variables are displayed with significance code: "ns" = $p > 0.1$; "." = $0.05 < p \leq 0.1$; "*" = $0.01 < p \leq 0.05$; "**" = $0.001 < p \leq 0.01$; "***" = $p \leq 0.001$. Each plot corresponds to one habitat: A) grassland, B) heathland, C) reed bed, D) salt marsh, E) sand dune, F) scrub, and G) woodland.

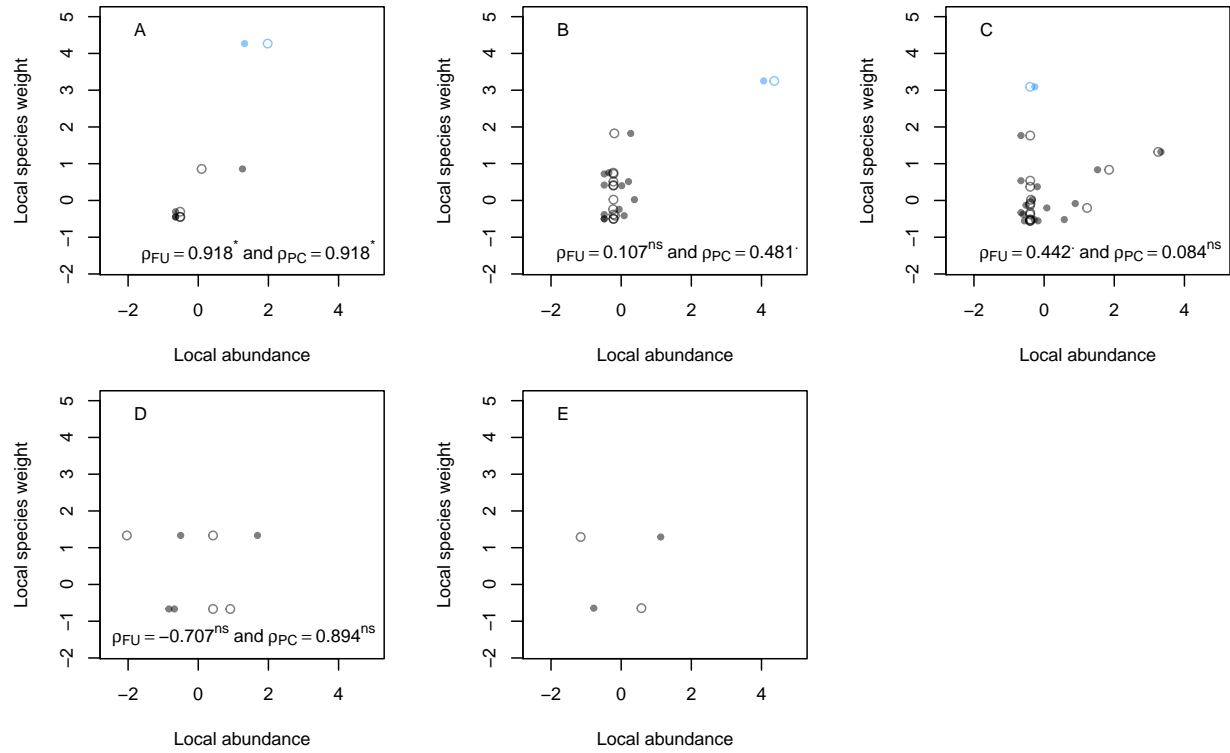


Figure S7.2: Within-habitat weight against the number of floral units (open circles) and against the percentage of cover (full circles) for Tautuku Peninsula. Each symbol corresponds to a plant species, and is coloured according to their role (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub). Estimated correlation coefficients (ρ_{FU} and ρ_{PC} for abundances estimated based on floral units and percentage cover respectively) between log-transformed variables are displayed with significance code: "ns" = $p > 0.1$; "." = $0.05 < p \leq 0.1$; "*" = $0.01 < p \leq 0.05$; "***" = $0.001 < p \leq 0.01$; "****" = $p \leq 0.001$. Each plot corresponds to one habitat: A) salt marsh, B) sand dune, C) *Corprosma* scrub, D) scrub Mānuka, and E) woodland.

Appendix S8: Are parasitoids' roles determined by their hosts?

The $\{z_i, c_i\}$ -values of a given parasitoid's hosts were calculated as the weighted arithmetic means of hosts' $\{z_i, c_i\}$ -values, and weights were based on the proportion of individuals of the focal parasitoid species which parasite each host species.

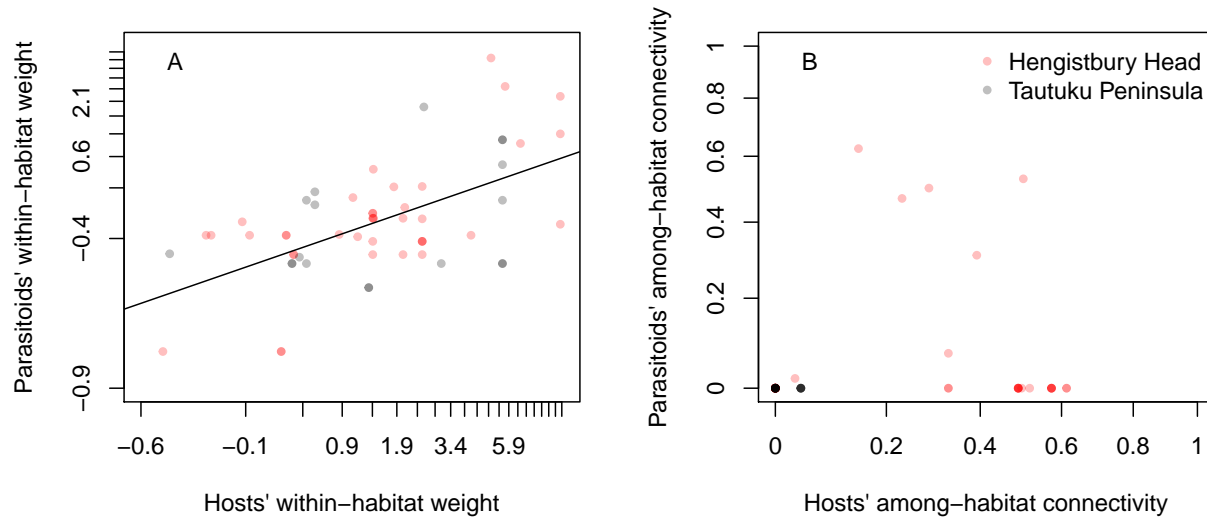


Figure S8.1: A) Within-habitat weight of parasitoids against those of their hosts (weighted arithmetic mean) with the regression represented with a solid black line, and B) Among-habitat connectivity of parasitoids against those of their hosts (weighted arithmetic mean). Each symbol corresponds to a parasitoid species, with those observed at Hengistbury Head coloured in red while those observed at Tautuku peninsula are shown in black.

For the regression between parasitoids' within-habitat weight and their hosts (weighted arithmetic mean, Fig. S8.1), we visually verified homoscedasticity and normality of the residuals after log-transforming data.

Appendix S9: Qualitative analysis of landscape roles

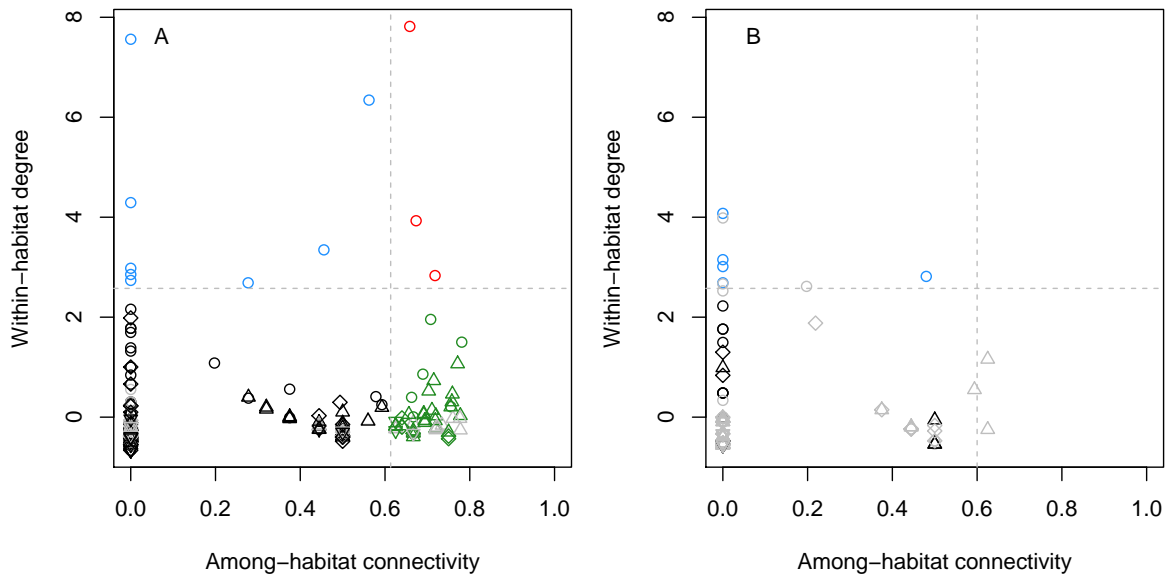


Figure S9.1: Species distribution in a $\{z_i, c_i\}$ -plane (within-habitat degree against among-habitat connectivity) according to the qualitative networks for A) Hengistbury Head, and B) Tautuku Peninsula. Each symbol corresponds to a species: open circles for plants, upward triangles for flower visitors, diamonds for herbivores, downward triangles for parasitoids, and asterisks for insects involved in multiple interaction types. Symbol colour refers to the landscape role to which it has been assigned (black: peripheral, green: habitat connector, red: landscape hubs, blue: habitat hubs) if its position in the plane is significantly different than expected according to the null model; otherwise the symbol is shown as grey.

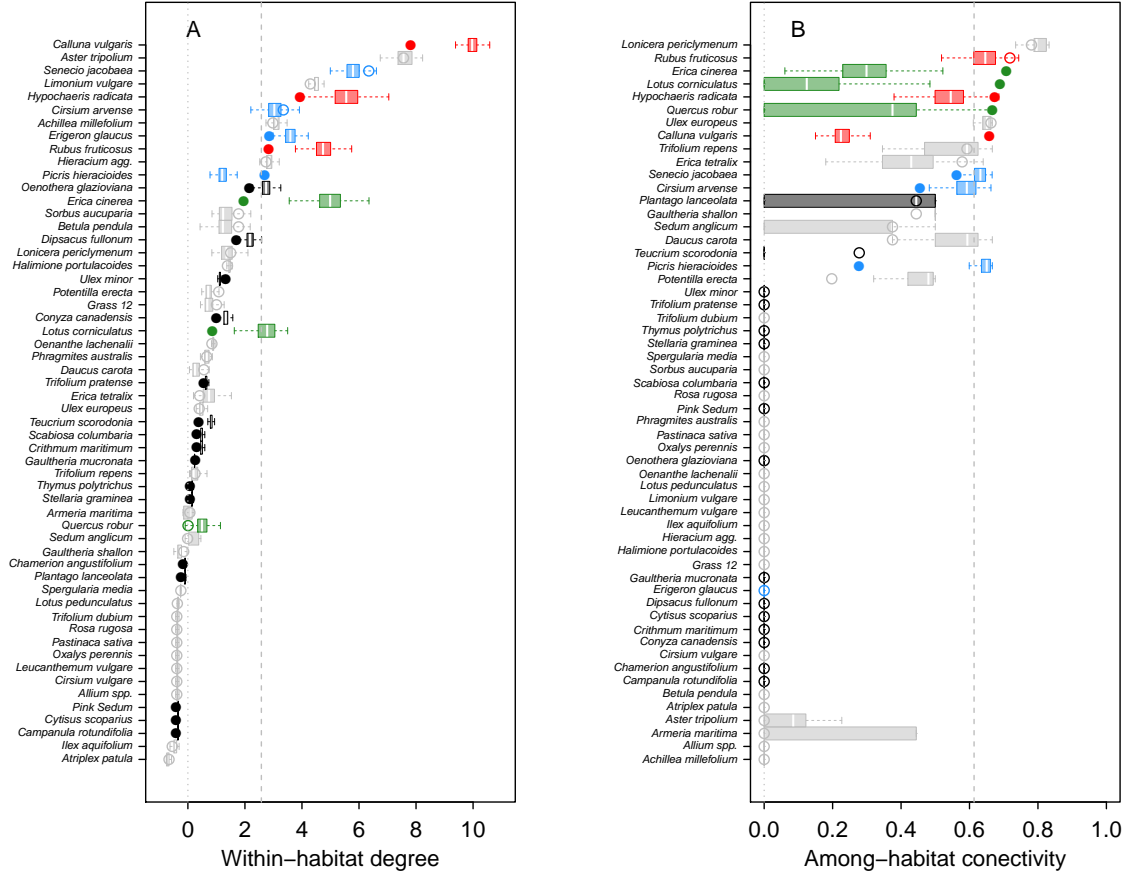


Figure S9.2: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of all plant species in Hengistbury Head. Plant species are ranked by descending observed values. Boxplots represent the distribution of expected values. Observed values are represented by an open circle if not different from expected in the null model, and by a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the species role to which it has been assigned (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected; otherwise the symbol is shown as grey.

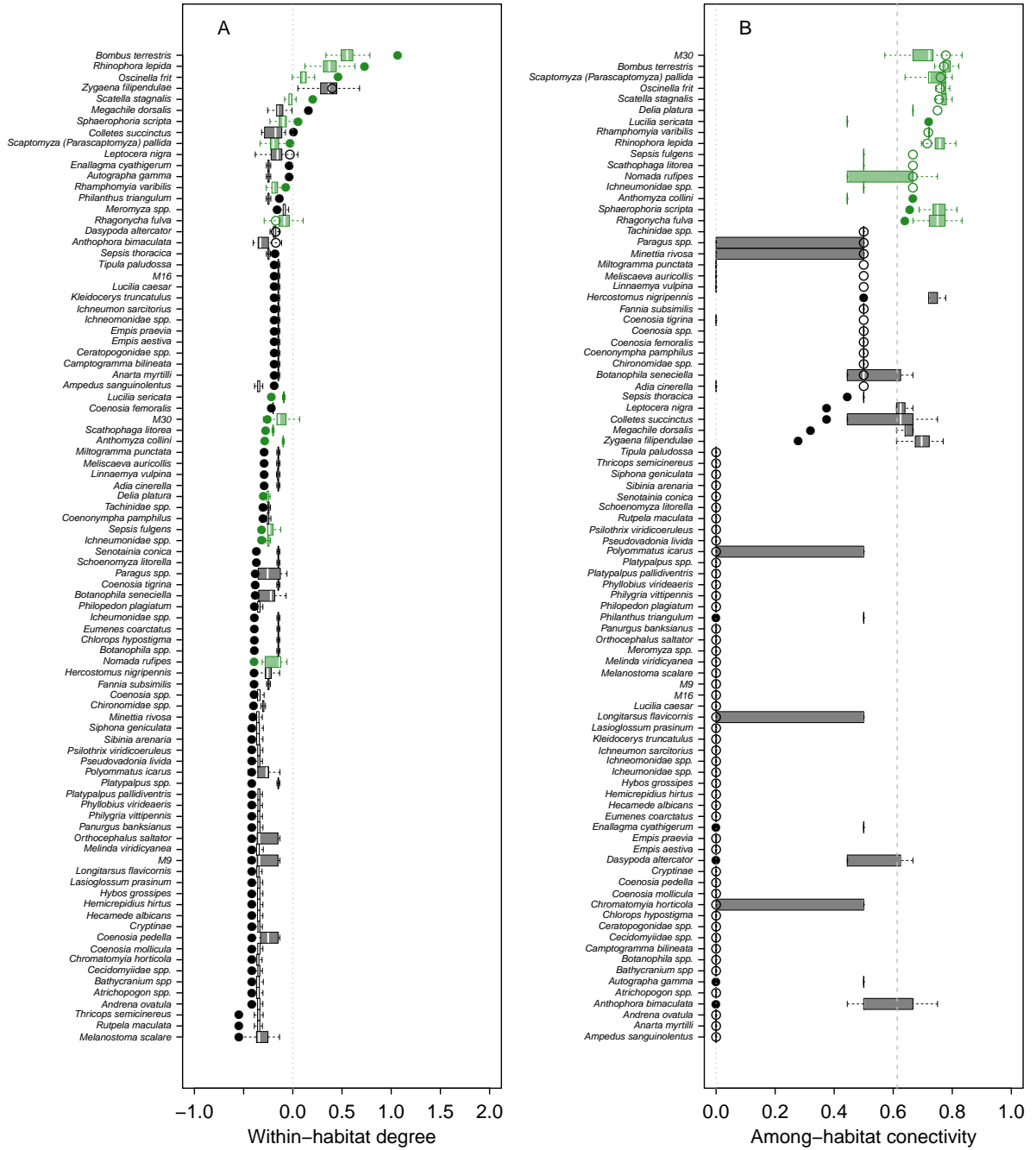


Figure S9.3: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of flower visiting species in Hengistbury Head. Insect species are ranked by descending observed values. Boxplots represent the distribution of expected values. Observed values are represented by an open circle if not different from expected in the null model, and by a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the species role to which it has been assigned (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are represented.

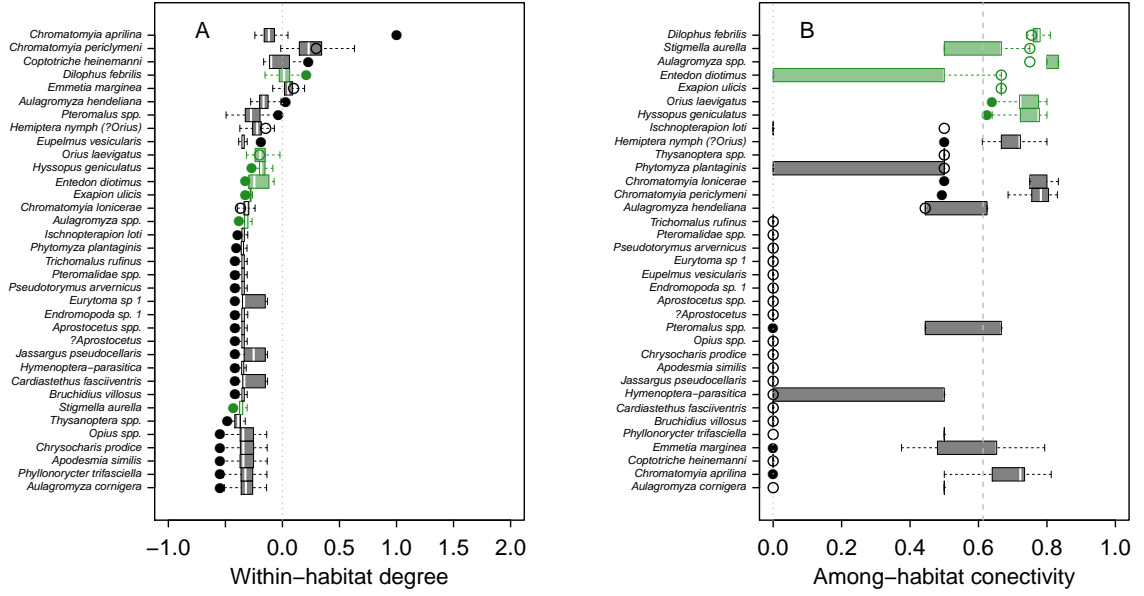


Figure S9.4: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of herbivores and parasitoids at Hengistbury Head (leaf-miners, seed-feeding insects, parasitoids). Insect species are ranked by descending observed values. Boxplots represent the distribution of expected values. Observed values are represented by an open circle if not different from expected in the null model, and by a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the species role to which it has been assigned (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are represented.

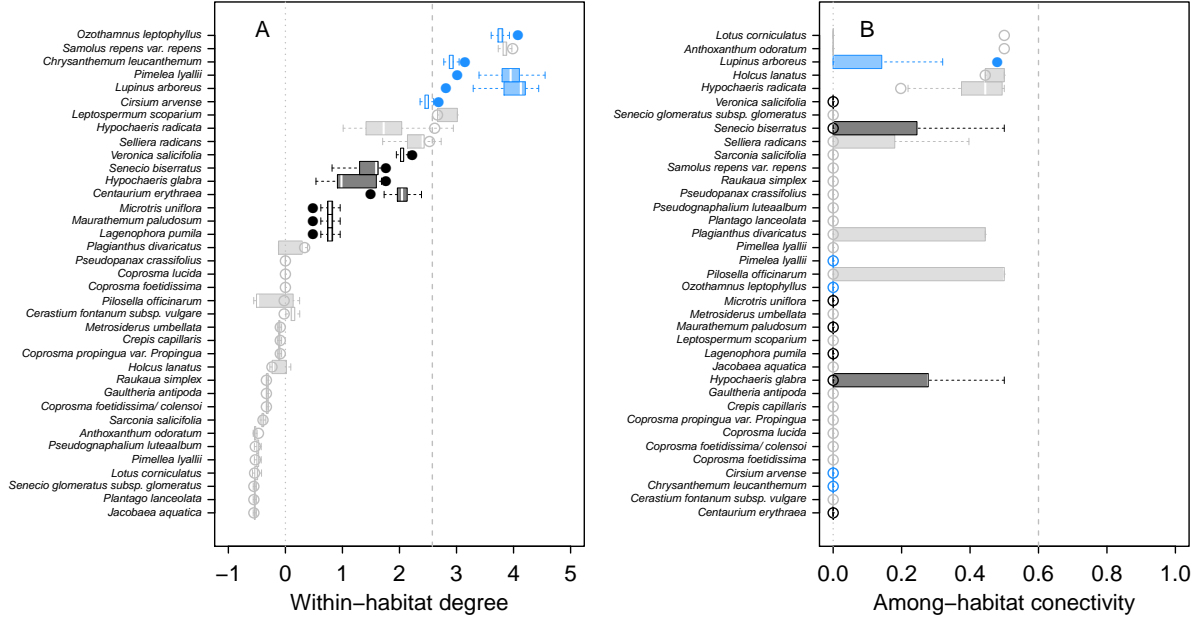


Figure S9.5: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of all plant species in Tautuku Peninsula. Plant species are ranked by descending observed values. Boxplots represent the distribution of expected values. Observed values are represented by an open circle if not different from expected in the null model, and by a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the species role to which it has been assigned (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub) if its position in the plane is significantly different than expected; otherwise the symbol is shown as grey. Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are represented.

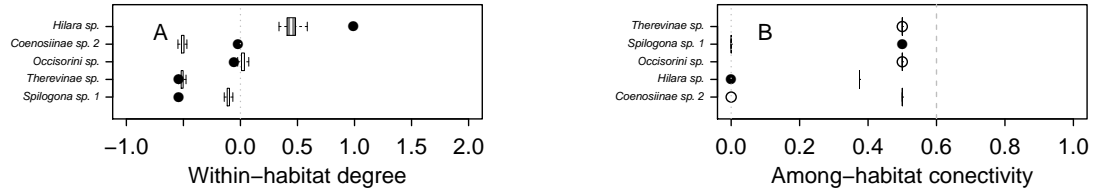


Figure S9.6: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of flower visiting species in Tautuku Peninsula. Insect species are ranked by descending observed values. The expected values for each are presented with boxplots. Observed values are represented by an open circle if not different from expected in the null model, and by a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the species role to which it has been assigned (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are represented.

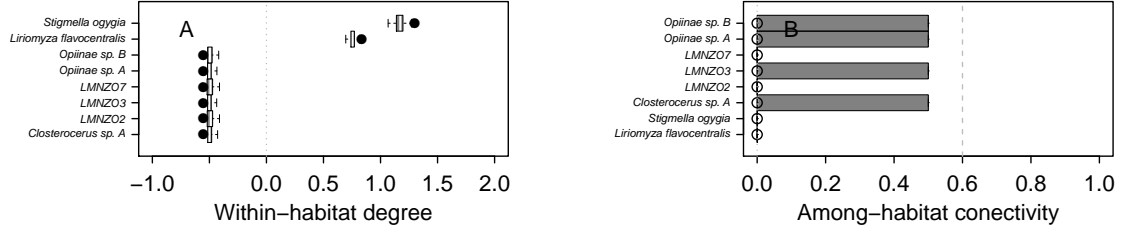


Figure S9.7: A) Within-habitat weight z_i and B) among-habitat connectivity c_i of other insect species in Tautuku Peninsula (leaf-miners, seed-feeding insects, parasitoids). Insect species are ranked by descending observed values. The expected values for each are presented with boxplots. Observed values are represented by an open circle if not different from expected in the null model, and by a filled circle otherwise. Outliers are not displayed to avoid confusion with observed values. The colour code refers to the species role to which it has been assigned (black: peripheral, green: habitat connector, red: landscape hub, blue: habitat hub). Only species which are significantly positioned in the $\{z_i, c_i\}$ -plane are represented.

Appendix S10: Effect of sampling effort on the measurement of species roles in landscape-scale networks

To investigate how sampling effort could affect species roles in the landscape, we calculated the within-habitat weight and among-habitat connectivity for 12 species with varying levels of sampling effort (from 50 to 2,236 individuals in Hengistbury Head, and from 50 to 575 individuals in Tautuku Peninsula). For a given sampling effort, we generated 100 networks from the pool of individual interactions observed in the field. All networks shared a selected subset of species which had different roles in the full dataset (i.e. four habitat hubs, one landscape hub, four connectors and three peripheral species in Hengistbury Head; and four habitat hubs, and eight peripheral species in Tautuku Peninsula). We performed this sensitivity analysis both for Hengistbury Head (Fig. S10.1) and Tautuku Peninsula (Fig. S10.2).

Increasing the sampling effort can lead to greater within-habitat weight values. This is particularly true for hub species, yet connectors and peripheral species show little within-habitat weight variation (Fig. S10.1A and Fig. S10.2A). Therefore, increasing the sampling effort could increase the likelihood of detecting hubs. Species ranking based on their within-habitat weight remains the same along the gradient of sampling effort, which highlights that potential hubs are still discernible even with a low sampling effort.

Among-habitat connectivity of connectors and peripherals is more sensitive to the sampling effort, as the position of these species in the $\{z_i, c_i\}$ -plane may change greatly with respect to hub species (Fig. S10.1B and Fig. S10.2B). Hence, the identification of habitat connectors relies on a high sampling effort in the field.

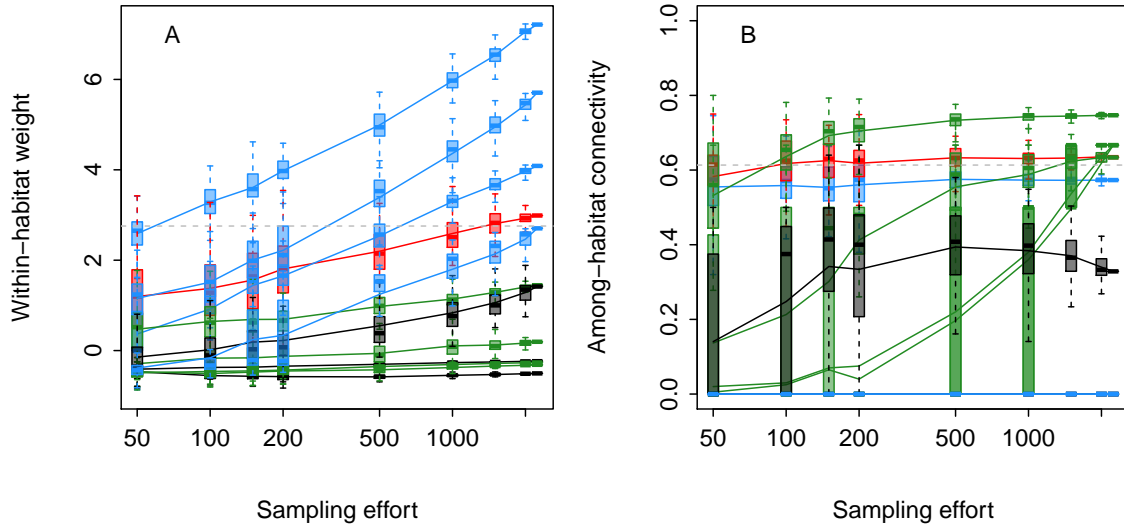


Figure S10.1: A) Within-habitat weight and B) among-habitat connectivity against sampling effort for a subset of species in Hengistbury Head. The sampling effort is defined by the number of individuals caught interacting in the field. Each boxplot connected with a line corresponds to one species. The colour indicates the species' roles as determined from the full dataset: habitat hubs are coloured in blue, landscape hubs in red, habitat connectors in green, and peripherals in black. Horizontal dashed lines show the thresholds discriminating, A) hubs (habitat and landscape hubs) from non-hub species (peripherals and habitat connectors), and B) connectors (landscape hubs and habitat connectors) from non-connector species (peripherals and habitat hubs.)

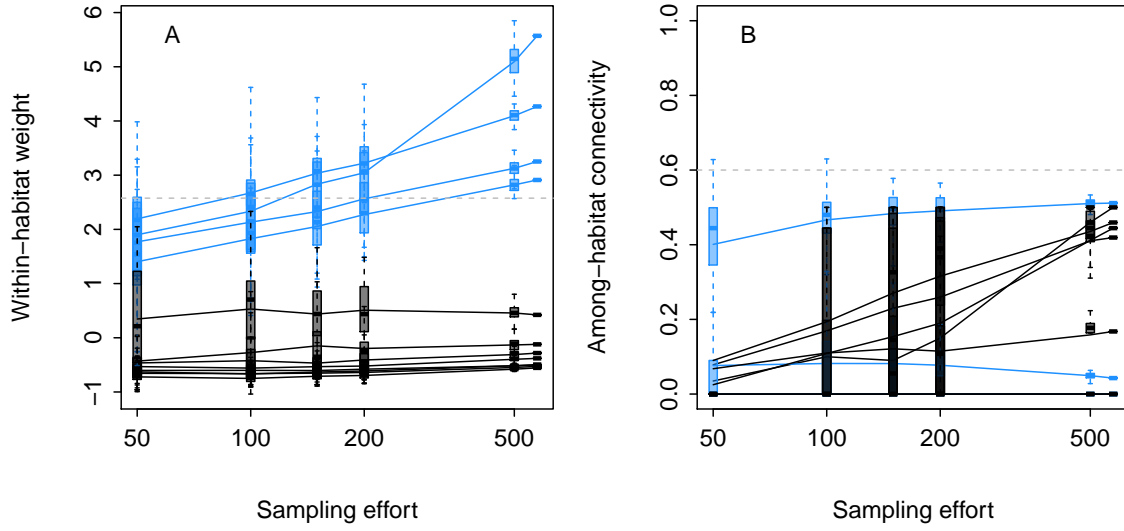


Figure S10.2: A) Within-habitat weight and B) among-habitat connectivity against sampling effort for a subset of species in Tautuku Peninsula. The sampling effort is defined by the number of individuals caught in the field sampling. Each boxplot connected with a line corresponds to one species. The colour indicates the species' roles as measured with the full dataset: habitat hubs are coloured in blue and peripherals in black. Horizontal dashed lines show the thresholds discriminating, A) hubs (habitat and landscape hubs) from non-hub species (peripherals and habitat connectors), and B) connectors (landscape hubs and habitat connectors) from non-connector species (peripherals and habitat hubs).

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